European shag diet and demography at a North Sea colony over half a century of environmental change

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Richard John Howells

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Candidate's declaration

I declare that the work contained in this thesis is entirely my own, unless otherwise stated, and it is of my own composition. Although I contributed to data collection throughout my PhD, the data utilised in this thesis was collected as part of the Isle of May Long Term Study, and before that under the direction of Professor Mike Harris and Professor Sarah Wanless in conjunction with the Isle of May Bird Observatory. No part of this work has been submitted for a degree at the University of Liverpool or any other University. All sources of information have been acknowledged by reference to the original authors.

Richard John Howells

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ABSTRACT

The earth's climate is changing rapidly, with pronounced impacts observed in all well studied ecosystems throughout the globe. Climate-mediated impacts are particularly marked and rapid within marine ecosystems. At the apex of such systems, marine top predators, such as seabirds, are vulnerable to direct and indirect climate-mediated effects, which may alter foraging capacity and prey availability. Consequently, many seabird populations are displaying pronounced changes in diet composition and declining demographic trends, yet the mechanisms underpinning these responses remain largely untested.

Although many studies have quantified seabird diet during the breeding season, the climate-related mechanisms determining long-term trends in diet composition are less well understood. Further, as the majority of seabird mortality occurs during winter, the diet of seabirds in winter is a key knowledge gap. Demographic trends have also been observed in numerous seabird species but, as with diet, we have limited understanding of the key mechanisms whereby climate is driving these trends. Finally, analyses of climate have focussed on broad scale processes, yet variation in microclimate may also be a key determinant of fine-scale distribution and demography within seabird colonies, yet this potential factor has been overlooked.

As a long-lived species with highly variable demography and plastic foraging habits, the European shag *Phalacrocorax aristotelis* provides an ideal species to investigate the impacts of environmental change on marine top-predator demography. This thesis uses demographic and diet datasets collected from a shag population breeding on the Isle of May, southeast Scotland, over half a century. By combining these data with environmental covariates, collected over a range of temporal and spatial scales, I quantify the response of this population to pronounced environmental change within the North Sea over the last five decades.

My thesis reveals that the diet of nestling shags in this population has changed dramatically over this period, from an almost complete dependence on lesser sandeel *Ammodytes marinus* to a range of prey types. Crucially, a suite of environmental covariates, including daily wind and long-term ocean warming, has contributed to this change in diet. The diet in winter displayed similar temporal trends (reduced sandeel and greater diversity). However, I found that the reduction in sandeel occurrence was more marked during the non-breeding period, with potential demographic consequences. I also documented a substantial increase in productivity and rapid phenological advancement over the last half a century. Crucially, the productivity trend was linked to this advancing phenology, which in turn was determined by conditions experienced in late winter and in the previous breeding season. Finally, pronounced fine-scale distributional trends occurred in this colony, with an increasing proportion of individuals breeding on the north-east side of the island, showing more rapid improvements in reproductive output than the declining sub-colonies in the south-west. This redistribution may benefit the population since exposure is a key factor in productivity and the prevailing wind direction is westerly. Overall, these results suggest that substantial dietary and demographic plasticity in shags may confer some resilience in this species to predicted future climate-mediated environmental change.

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Chapter 1: General Introduction

"In all things of nature, there is something of the marvellous."– Aristotle, 350 BC

GLOBAL ENVIRONMENTAL CHANGE

Anthropogenic climate change, linked to increasing emissions of greenhouse gases (CO_2, CH_4) and consequent global warming, is considered one the principal threats to global biodiversity (IPCC, 2014). Ecological impacts of climatic change have been observed in all well-studied marine, freshwater and terrestrial systems across the globe, ranging from temperate forests to arctic tundra and tropical coral reefs (Walther *et al.*, 2002; Parmesan, 2006). Climate change can affect organisms via two principle mechanisms; indirect and direct effects (Thomas, 2010). Indirect climatic effects occur where long-term changes in mean environmental conditions, such as temperature, affect species indirectly via bottom-up effects on trophic levels altering the structure and functioning of ecosystems (Parmesan and Yohe, 2003; Root *et al.*, 2003; Tylianakis *et al.*, 2008). These trophic interactions, along with species specific thermal tolerances, can lead to range shifts, in particular to higher latitudes and/or elevations, which have been observed in many taxonomic groups (Parmesan and Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006; Thomas, 2010). However, responses are species-specific with range expansions to lower latitudes and elevations also recorded (Thomas, 2010). Direct effects occur where climate affects the demographic rates of species as opposed to their resources. For example, the frequency and severity of extreme weather events is increasing, leading to direct effects on fitness and population processes (Parmesan, Root and Willig, 2000; Moreno and Moller, 2011). As well as immediate effects of direct and indirect climatic change on recruitment, growth or survival, conditions experienced at one point in time may have downstream fitness consequences in future seasons via lagged or carry-over effects (Norris, 2005; Harrison *et al.*, 2011). Although the impacts of climatic change on many organisms are well documented, the mechanisms underpinning these effects are less well understood. This is a key issue, as in many systems these climate-mediated changes are predicted to increase in the future, associated with increases in mean temperature and the frequency and magnitude of extreme weather events (Easterling *et al.*, 2000; McInnes, Erwin and Bathols, 2011; IPCC, 2014). Thus, as climate-mediated ecosystem changes are likely to continue and potentially intensify, there is an urgent need to develop further our

understanding of the mechanistic links between climate, ecosystems and the fitness consequences on species.

SEASONALITY

Due to the earth's orbit around the sun and pronounced axial tilt, temperate and polar regions receive marked variations in solar radiation throughout the year (Thomson, 1915). This leads to pronounced seasonal differences in environmental conditions across the annual cycle. Temperate zones display strong seasonality, in which peak resource availability during spring, linked to heightened primary productivity, provides a period suitable for growth and reproduction, when energetic demands increase (Lack, 1968; Perrins, 1970; Drent and Daan, 1980). As such, in temperate regions many species have evolved to coincide breeding with these periods of resource availability or favourable climatic conditions (Daan and Tinbergen, 1991; Stearns, 1992; White, 2008). For example, Great Tits *Parus major* time their reproduction to coincide with seasonal peaks in caterpillar abundance (Van Noordwijk *et al.* 1995), while Canada geese *Branta canadensis* breed when vegetation nitrogen content is high enough for successful chick rearing (Sedinger and Raveling, 1986). Optimal timing of peak demand and resource availability has positive fitness consequences, including increased fecundity and adult survival (Thomas *et al.*, 2001).

TROPHIC MISMATCH

One of the most ubiquitous and conspicuous hallmarks of climate change in natural ecosystems, but particularly in seasonal environments, is the shift in the timing of key biological events, in particular breeding phenology (Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006). Globally, there is a general trend towards phenological advancement i.e. biological events are getting earlier (Parmesan and Yohe, 2003; Root *et al.*, 2003; Thackeray *et al.*, 2016). However, climate change may affect demography if it alters the relative timing between peak demand and resource availability (Visser and Both, 2005; Visser, Holleman and Gienapp, 2006; Mayor *et al.*, 2017). Many species are unable to advance at the same pace as their resources (Thackeray *et al.*, 2010), because

different trophic levels respond to climatic change at different rates (Durant, Anker-Nilssen and Stenseth, 2003; Durant *et al.*, 2007; Both *et al.*, 2009). As such, successive trophic levels can become mismatched in time (hereafter trophic mismatch), with substantial consequences for reproductive success, recruitment and survival of consumers (Post *et al.*, 2001; Miller-Rushing *et al.*, 2010). Even where species advance their phenology, physiological constraints may limit their capacity to match resource availability. For example, although barnacle geese *Branta leucopsis* have advanced their spring arrival date to keep pace with their rapidly warming arctic breeding grounds, the energetic costs of early arrival extend the time to laying, and so the peak in resource availability is missed, reducing offspring survival (Lameris *et al.*, 2018).

The concept of trophic mismatch was first used in reference to inter-annual variability in cod *Gadus morhua* recruitment due to overlap with planktonic blooms (Hjort, 1914; Cushing, 1975, 1990), but has subsequently been adopted into the climate change literature (Visser and Both, 2005). Trophic mismatch theory has been used to describe a wide range of climate-altered biotic interactions including: plant/caterpillar/bird (Visser, Holleman and Gienapp, 2006); arctic vegetation/waterfowl (Doiron, Gauthier and Levesque, 2015), invertebrate/shorebird (van Gils *et al.*, 2016), fish/seabird (Durant *et al.*, 2005) and goose/bear (Gormezano and Rockwell, 2013). As trophic mismatch can also influence individual condition, effects experienced at one point in time may have downstream fitness consequences in future seasons via early life or carry-over effects (van Gils *et al.*, 2016). Trophic mismatch has now been observed in many terrestrial and aquatic environments and it is widely accepted that this process is exerting strong, pervasive and persistent effects on the functioning of marine ecosystems across the globe (Edwards and Richardson, 2004).

MARINE ENVIRONMENTAL CHANGE

Approximately 72% of the world's surface is covered by oceans (Hays, Richardson and Robinson, 2005), yet only ~14% are considered untouched wilderness (Jones *et al.*, 2018). Thus, many of these marine environments are changing rapidly due to a

multitude of anthropogenic pressures including over-harvesting, pollution, and habitat modifications (Brierley and Kingsford, 2009; Halpern, 2009; Hoegh-Guldberg and Bruno, 2010; Elliott and Elliott, 2013). Top-down pressures, such as industrial fish extraction, and bottom-up processes associated with ocean warming, are affecting marine organisms at multiple trophic levels (Lynam *et al.*, 2017). Further, human debris, predominantly plastic waste, is a ubiquitous and increasing component of marine ecosystems across the globe, with over 690 marine species estimated to have been affected (Gall and Thompson, 2015). However, despite slower warming in the oceans than land (IPCC, 2014), climate-mediated effects are a dominant driver of marine environmental change, and are fundamentally altering marine ecosystems across the globe (Hoegh-Guldberg and Bruno, 2010; Poloczanska *et al.*, 2013). Many marine environments are also displaying faster rates of change than terrestrial systems (Burrows *et al.*, 2011), which may limit the capacity of higher trophic organisms to keep pace. Natural, decadal-scale climate variation, such as the North Atlantic Oscillation and Southern Oscillation, also have pronounced impacts on marine food-webs (Barber and Chavez, 1983; Ottersen *et al.*, 2001; Stenseth *et al.*, 2002; Mills *et al.*, 2008), and may compound or mitigate anthropogenic effects. Regime shifts - abrupt, persistent changes in the structure and function of ecosystems - are also widely reported in marine environments in response to both natural and anthropogenic drivers (Anderson and Piatt, 1999; Beaugrand, 2004; Brierley and Kingsford, 2009). As a consequence of these combined effects, it has been suggested that we are on the precipice of a global mass extinction of marine taxa (McCauley *et al.*, 2015). If these threats and ongoing erosion of marine biodiversity continue unabated, there is the potential for catastrophic ecological and societal consequences (Worm *et al.*, 2006). Therefore, there is an urgent need to quantify the effects of both anthropogenic and natural drivers on marine environments to develop a mechanistic understanding of marine ecosystem change.

MARINE TOP PREDATORS

At the apex of marine ecosystems, marine top predators, including fish, cetaceans, pinnipeds and seabirds are vulnerable to a multitude of anthropogenic impacts, including introduced predators (Jones *et al.*, 2008), invasive species (Molnar *et al.*,

2008), pollution (Wilcox, Van Sebille and Hardesty, 2015; Worm, 2015), and direct and indirect fishing interactions (Worm *et al.*, 2009; Croxall *et al.*, 2012). However, climate-mediated environmental change is having pronounced impacts on marine top predators throughout the globe (Hobday *et al.*, 2015). Climatic impacts on marine top predators typically operate via the bottom-up effects of ocean warming on lower trophic levels, in particular plankton, and associated changes in the abundance, distribution and energetic value of mid-trophic level fish, which are key prey for a guild of top predators (Cury *et al.*, 2000; Beaugrand *et al.*, 2003; Frederiksen *et al.*, 2006; Pikitch *et al.*, 2012). This is because multiple trophic levels are dependent on seasonal pulses in plankton abundance, which are tightly linked to climatic conditions (Aebischer, Coulson and Colebrookl, 1990; Cushing, 1990; Edwards and Richardson, 2004). Thus, climate mediated changes in focal prey populations is a key mechanism driving climatic impacts on marine top predators via bottom-up effects (Hays, Richardson and Robinson, 2005; Dulvy *et al.*, 2008; Attrill, Wright and Edwards, 2010; ter Hofstede, Hiddink and Rijnsdorp, 2010; Doubleday *et al.*, 2016). In one of the first studies to identify correlations between climate and multiple trophic levels in marine systems, Aebischer *et al.* (1990) identified parallel long-term trends in the abundances of phytoplankton, zooplankton and herring *Clupea harengus*, and black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) breeding success. Subsequently, numerous studies have identified links between climate, lower trophic levels and a range of marine top predators (Croxall, Reid and Prince, 1999; Durant *et al.*, 2005; Burthe *et al.*, 2012; Fleming *et al.*, 2015). In addition to this, the increased frequency and severity of extreme weather eventsassociated with climatic change, along with more subtle changes in local weather, can also have negative impacts, through increased mortality or reduced reproductive output (Frederiksen *et al.*, 2008; Moreno and Moller, 2011; Descamps *et al.*, 2015; Newell *et al.*, 2015). Thus, marine top predators are vulnerable to a wide range of climate-mediated environmental impacts, but responses likely vary depending on the location and species in question (Frederiksen *et al.*, 2005; Frederiksen, Furness and Wanless, 2007; Sandvik, Erikstad and Sæther, 2012), and may display a temporal lag of days, weeks or even years (Reid and Croxall, 2001; Thompson and Ollason, 2001; Ito *et al.*, 2009). Although marine top predators may be affected by current and lagged

conditions at the same time, which may be operating over a range of spatial and temporal scales, few studies have quantified responses simultaneously. However, such analyses are crucial if we are to understand the relative importance of current and lagged drivers on ecosystem processes and linked top predator demography.

SEABIRDS

Seabirds are highly visible and charismatic components of many marine environments, providing numerous provisioning and cultural ecosystem services (Burdon *et al.*, 2017). As top predators in marine systems, seabirds have evolved a suite of life history characteristics that allow them to thrive in these often harsh and challenging locations (Lack, 1968; Schreiber and Burger, 2002). For example, all seabird species are relatively long-lived, have high survival rates (in excess of 90% in many species) and low fecundity (generally one clutch per year of 1-4 eggs; Schreiber & Burger 2002). Further, the majority of seabirds (95%) breed colonially, are strongly philopatric and display high monogamy (Danchin and Wagner, 1997; Coulson, 2002). Collectively, these features are referred to as the "Seabird Syndrome", some of which at least, all seabirds share (Gaston, 2004).

Globally, seabirds are estimated to consume approximately 70 million tons of marine prey annually (Brooke, 2004). Although marine fish are the primary prey of most populations (Shealer, 2002), seabirds consume a wide range of resources, including human waste and fisheries discards (Pierotti and Annett, 1991; Votier *et al.*, 2008), jellyfish (McInnes *et al.*, 2017), cephalopods (Croxall and Prince, 1996) and zooplankton (Springer, Byrd and Iverson, 2007; Bond *et al.*, 2011). Foraging depths are highly variable, ranging from a few centimetres to over half a kilometre below the ocean surface (Kooyman *et al.*, 1971), while feeding behaviours include plunge diving, pursuit diving, suction feeding, kleptoparasitism, avian predation and scavenging (Oro, Pradel and Lebreton, 1999; Votier *et al.*, 2010; Blight *et al.*, 2015; Enstipp *et al.*, 2018).

Due to their relative accessibility when breeding on land, seabird demography has been the subject of substantial scientific enquiry. As long-lived species, with low mortality, reproductive output is the seabird demographic parameter considered

most vulnerable to changes in environmental conditions (Cairns, 1987). This is because as iteroparous breeders, seabirds may forgo reproduction or reduce breeding effort under poor environmental conditions, in order to maintain individual condition and enhance lifetime fitness (Drent and Daan, 1980; Stearns, 1992). Numerous environmental factors have been shown to be related to seabird breeding success, including large-scale climatic indices, such as the North Atlantic Oscillation, local climatic conditions, such as Sea Surface Temperature and weather, and predation (Aebischer, 1993; Oro, Pradel and Lebreton, 1999; Whittam and Leonard, 1999; Thompson and Ollason, 2001; Frederiksen, Furness and Wanless, 2007; Sherley *et al.*, 2012). For example, the breeding success of some UK seabird species is correlated with the NAO, while in others SST and stratification is important (Frederiksen, Harris, *et al.*, 2004; Carroll *et al.*, 2015). Crucially, these climatic effects are considered to operate primarily on breeding success indirectly, through effects on prey availability, quality and distribution, although impacts on seabird foraging capacity are also important (Montevecchi and Myers, 1996; Durant *et al.*, 2007; Ito *et al.*, 2009). Nest site characteristics, such as height and exposure, and location are also important and may affect the relative vulnerability of nests to local climatic conditions, such as prevailing wind and rain (Stokes and Boersma, 1998; Hamer, 2002; Velando and Freire, 2003; Córdoba-Córdoba, Ouyang and Hauck, 2010; Bonter *et al.*, 2014). Intrinsic effects, including phenology, density dependence, competition, age/experience, and carry-over effects can also affect seabird reproduction (Kokko, Harris and Wanless, 2004; Daunt *et al.*, 2007; Thomas E Reed *et al.*, 2008; Renner *et al.*, 2014). For example, breeding success in northern fulmars *Fulmarus glacialis* is negatively affected by current and lagged winter NAO but positively related to past breeding success, the effect of which is mediated by pair bond duration (Lewis *et al.*, 2009). Another study in this species also highlighted the importance of lagged effects, with breeding success higher following negative North Atlantic Oscillation values in the winter prior to breeding and juvenile recruitment linked to early life conditions experienced in the year of birth, with the effect on colony size lagged by 5 years (Thompson and Ollason, 2001). Ultimately, however, prey availability and linked diet composition are likely to be the key determinants of seabird productivity in most

situations (Cairns, 1987), and provide the mechanism through which many of these environmental and intrinsic factors operate.

SEABIRD DIET

Numerous methods exist to investigate the diet of seabirds (reviewed in Barret *et al.* 2007). These include lethal sampling (Lumsden and Haddow, 1946; Blake, 1984; Harris *et al.*, 2015), Fatty Acid analysis (Ronconi and Burger, 2008; Owen *et al.*, 2013), DNA (McInnes *et al.*, 2016; Komura *et al.*, 2018) and Stable Isotope Analysis (Flemming and van Heezik, 2014; Blight *et al.*, 2015). However, the most widely used method is involves collecting regurgitated food, either in the form of stomach contents or pellets (Pierotti and Annett, 1991; Green *et al.*, 2015). Being relatively easy to observe, collect and identify, particularly during breeding, seabird diet composition has received much attention in the scientific literature (Steven, 1933; Harris and Hislop, 1978; Croxall, Reid and Prince, 1999; Chiaradia, Costalunga and Kerry, 2003; Davoren *et al.*, 2012; Blight *et al.*, 2015), with several datasets extending over many decades (Anderson *et al.*, 2014; Green *et al.*, 2015; Riordan and Birkhead, 2018). Seabird diet composition may reflect prey availability (Barrett *et al.*, 2007), which fluctuates over space and time in response to environmental conditions, including climate (Montevecchi and Myers, 1996; Lewis, Wanless, *et al.*, 2001; Ito *et al.*, 2009; Gaston and Elliott, 2014) and weather (Sagar and Sagar, 1989; Finney, Wanless and Harris, 1999; Elliott *et al.*, 2013). Foraging preference is also important, as species will preferentially feed on a particular prey type at a greater level than its relative availability (Martin, 1989; Litzow, Piatt, Abookire, *et al.*, 2004). For example, guillemots *Uria aalge* are able to maintain consistent chick energetic intake, despite fluctuating abundances of their two focal prey, lesser sandeel *Ammodytes marinus* (*hereafter* sandeel) and sprat *Sprattus sprattus* (Smout *et al.*, 2013). However, due to behavioural specificity and foraging constraints, some species are unable to switch during periods of reduced prey availability, with specialist species likely to be more affected than generalists (Martin, 1989; Hamer, Furness & Caldow, 1991). For example, Martin (1989) demonstrated that between 1973 and 1988, during a period of low sandeel availability, northern gannet *Morus bassanus* switched to alternative prey, whereas Atlantic puffins *Fratercula arctica* (hereafter puffin) did not. Thus, diet

composition in seabirds is determined by a complex suite of mechanisms, which vary between species, locations and over time.

Throughout the breeding period, seabirds act as central-place foragers, returning regularly to the colony in order to defend nests and feed offspring (Orians & Pearson 1977). This may constrain the prey and habitats available to foraging parents, with individuals particularly vulnerable to prey variability during this time (Martin, 1989; Monaghan *et al.*, 1989; Furness and Tasker, 2000; Reid and Croxall, 2001). Breeding birds are also subject to enhanced energetic demands during this period, due to the costs of mate acquisition, nest site defence, egg production and provisioning the brood (Drent and Daan, 1980; Enstipp *et al.*, 2010). This may limit the capacity for birds to adjust their foraging behaviour, further amplifying the effects of fluctuating prey availability in response to environmental change.

Numerous studies have demonstrated that prey availability and linked diet composition affects seabird breeding success (Pierotti and Annett, 1990; Crawford and Dyer, 1995; Davis, Nager and Furness, 2005; Furness, 2007). In two landmark studies Monaghan *et al.* (1989, 1992) showed that a reduction in the dietary contribution and size of sandeel was responsible for reproductive failure in Arctic terns *Sterna paradisaea*. Similarly, the proportion of gravid capelin *Mallotus villosus* in guillemot chick diet is related to offspring condition and overall fledging success (Davoren and Montevecchi, 2003). Prey quality is also important, with lower calorific content in focal prey implicated in breeding failure (Annett and Pierotti, 1999; Wanless *et al.*, 2005; Österblom *et al.*, 2008). However, diet change may have positive impacts, as in rhinoceros auklets *Cerorhinca monocerata*, where an abrupt change in zooplankton community composition was reflected in diet composition and linked increases in breeding success (Hedd *et al.*, 2006). Crucially, a reduction in the contribution of a dominant prey type may not always reduce breeding success if there is no overall change in the quality of alternative prey (Chiaradia, Costalunga and Kerry, 2003). Even where the diets of breeding seabirds are well understood, the direct and indirect drivers of diet composition, along with the temporal scales over which effects operate, are not known in the vast majority of seabird species. Given that diet composition is a key determinant of seabird demography, understanding

the links between diet and environmental conditions, over a range of temporal scales is thus a priority.

Although seabird breeding diet has been studied extensively, practical constraints of obtaining diet samples away from the nest and outside the breeding season mean that little is known regarding the diet of seabirds outside the breeding period (Barrett *et al.*, 2007). Those studies which have been conducted have generally demonstrated marked differences from that of breeding (Sonntag and Hüppop, 2005; Harris *et al.*, 2015), due to a combination of altered prey availability (Kowalczyk *et al.*, 2015), energetic constraints (Markones, Dierschke and Garthe, 2010) and habitat associations (Ainley *et al.*, 1996). Seabird diet composition outside the breeding season may affect demographic parameters, including phenology and survival (Oro and Furness, 2002; Davis, Nager and Furness, 2005; Sorensen *et al.*, 2009). Indeed, as the majority of seabird mortality occurs during winter (Weimerskirch, 2002), our limited understanding of seabird diet throughout the annual cycle is a key knowledge gap. Moreover, given that a number of studies have demonstrated long-term changes in the diet of breeding seabirds (Miller and Sydeman, 2004; Gaston and Elliott, 2014; Green *et al.*, 2015), assessments of trends in the year-round diet of full-grown birds is urgently required, but is yet to be conducted for any seabird species.

SEABIRD INDICATORS

At the apex of marine systems, seabird foraging behaviour, productivity and population size, may track spatio-temporal variation in environmental conditions, notably prey abundance and availability (Frederiksen *et al.*, 2005). Further, as seabirds breed on land and often forage within marine hotspots, important for both biodiversity and fisheries, they have been proposed as accessible, reliable and cost-effective indicators of wider marine environmental conditions (Cairns, 1987; Piatt *et al.*, 2007; Durant *et al.*, 2009; Einoder, 2009). However, in order for seabirds to be used as indicators, it is essential to accurately quantify the relationship between the demographic parameter and environmental condition in question. To do this, detailed information on both seabird demography and independent data on

environmental conditions, such as prey abundance, is required (Durant *et al.*, 2009). Further, where responses are non-linear (Cury, Boyd, Bonhommeau, Anker-Nilssen, Robert J M Crawford, *et al.*, 2011), it may be difficult to relate the changes in a key demographic rate or diet (i.e. the indicator) and the environment (Durant *et al.*, 2009). Notwithstanding this, seabirds have been widely utilised as indicators for various wider environmental conditions. For example, kittiwake productivity has been used as an indicator of North Sea environmental change, including both climatic-forcing and fisheries pressures (Wanless *et al.*, 2007). Similarly, using a model incorporating the proportion of sardines in the diet of elegant terns *Sterna elagans*, the breeding success of Heermann's gull *Larus heermanni*, and SST in the area, Velarde, Ezcurra, Cisneros-Mata, *et al.*, (2004) were able to predict catch per unit effort in the sardine fishery of the Gulf of California, with an accuracy of 73%. Thus, by studying the links between seabird diet, demography and environmental conditions, we can gain a mechanistic understanding of the processes driving marine environmental change and use this information to develop suitable indicators of marine conditions.

SEABIRD THREATS

Seabirds are one of the most threatened groups of avian taxa globally (Croxall *et al.*, 2012), declining in abundance by 69.7% between 1950 and 2010 (Paleczny *et al.*, 2015). They face a number of anthropogenic pressures, both on land and at sea, including competition with fisheries, accidental bycatch, pollution and introduced predators (Lewison *et al.*, 2012). However, one of the most important factors underpinning the declines observed in many seabird populations are changes in the availability of key prey, notably forage fishes (Cury *et al.*, 2000; Pikitch *et al.*, 2012), either through top-down exploitation, bottom-up climate-mediated impacts or both (Reid and Croxall, 2001; Frederiksen, Furness and Wanless, 2007; Ainley and David Hyrenbach, 2010). For example, seabirds in the California Current System are affected by a multitude of pressures on their prey including bottom-up effects of climatic forcing and over-exploitation of prey stocks, in addition to competition with climate-mediated increases in baleen whale populations (Ainley and David Hyrenbach, 2010). Similarly, changes in the distribution of focal prey, associated with

overfishing and environmental change, are key drivers of seabird declines and redistribution in the Benguela ecosystem (Crawford, Makhado and Oosthuizen, 2017). However, environmental change can also bring ecological benefits, including increased prey abundance and diversity, or novel opportunities. For example, thick billed murres *Uria lomvia* are able to exploit high prey densities associated with the tentacles of the northern sea nettle *Chrysaora melanaster*, the abundance of which has increased due to ocean warming (Sato *et al.*, 2015). Thus, changes in key prey populations, whether through top-down or bottom-up mechanisms, can alter demographic processes and ultimately seabird population sizes (Baum and Worm, 2009). Additionally, numerous direct effects of anthropogenic climate-mediated change have been observed, including increased winter mortality and reduced reproductive output, linked to the increased frequency, magnitude of extreme weather events (Frederiksen *et al.*, 2008; Moreno and Moller, 2011; Bonter *et al.*, 2014; Descamps *et al.*, 2015; Newell *et al.*, 2015). Further, at a global scale, seabirds are not advancing their phenology in response to ocean warming, which may exacerbate any direct and indirect climate-mediated effects on focal prey populations (Keogan *et al.*, 2018). Therefore, there is an urgent need to better understand the links between seabird demography and environmental conditions, over a range of spatial and temporal scales, particularly within marine environments that are changing rapidly.

Recent technological advancements have greatly developed our understanding of seabird spatial distribution and threats at sea (Grémillet and Boulinier, 2009). For example, bio-logging has provided novel insights into the at sea distribution of adult seabirds during both the breeding and non-breeding periods (Lewis *et al.*, 2001; Bogdanova *et al.*, 2011; Alonso *et al.*, 2018), as well as the vast distances travelled by individual birds throughout the annual cycle and within individual foraging trips (Egevang *et al.*, 2010; Edwards *et al.*, 2013). However, much less is known regarding seabird spatial distribution and linked fitness consequences on land, yet this remains a key knowledge gap in our understanding of seabird population dynamics and trends. At the colony scale, breeding seabirds will experience broadly similar environmental conditions, such as climate or prey availability (Frederiksen, Mavor

and Wanless, 2007). However, within colony breeding distribution may result in fine-scale differences in environmental conditions due to the physical characteristics of different locations, such as height, exposure and slope (Lack, 1968; Harris *et al.*, 1997; Jones, 2001; Forster and Phillips, 2009). These differences can have important implications for reproductive output (Negro and Hiraldo, 1993; Harris *et al.*, 1997; Stokes and Boersma, 1998; Velando and Freire, 2003). Such differences may be particularly important during extreme weather events, with the orientation or exposure of nest locations determining susceptibility to negative effects (Boersma and Rebstock, 2014; Bonter *et al.*, 2014; Newell *et al.*, 2015). For example, on the Isle of May, Scotland, a severe summer storm had a more pronounced negative effect on a suite of seabird species nesting on the west of the island than those on the east (Newell *et al.*, 2015). Fine-scale breeding distribution is determined by a suite of mechanisms, including environmental conditions, conspecific attraction, and individual experience (Boulinier and Danchin, 1997; Boulinier *et al.*, 2008; Robert *et al.*, 2014). Thus, interannual variability and/or trends in any of these intrinsic and extrinsic factors may cause fine-scale distributional changes (Bonter *et al.*, 2014), with linked reproductive consequences. However, long-term trends in fine-scale, breeding distribution and the associated reproductive consequences are yet to be quantified in any seabird species, but are essential for understanding the impacts of environmental change within breeding colonies.

THE NORTH SEA

The North Sea is a temperate, relatively homogenous, shallow-shelf sea (<200 m depth; mean 70 m), characterised by strong seasonality, including an annual peak in phytoplankton abundance i.e. the spring bloom (Fransz *et al.*, 1991; Smayda, 1997; Edwards *et al.*, 2002). This bloom is of key ecological significance and either directly or indirectly influences all marine life within the region, via bottom-up effects (Daan, Bromley, Hislop 1990; Fransz *et al.* 1991; Miller 2004; Edwards & Richardson 2004). Large parts of the North Sea are highly productive 'wasp-waist' ecosystems, characterised by high species diversity at upper and lower trophic levels, but relatively few, yet highly abundant, mid-trophic species (Cury *et al.*, 2000; Fauchald *et al.*, 2011). Here small, planktivorous shoaling fish, notably sandeel, provide a key

trophic link channelling energy from plankton, through the system, to upper trophic levels (Dunnet *et al.* 1990; Cushing 1990; reviewed in McDonald *et al.* 2015).

Sandeels are non-migratory and within the North Sea exist at the southern limit of their critical thermal boundary (Frederiksen *et al.*, 2013). Sandeels display a preference for fine, sandy sediments (Wright, Jensen and Tuck, 2000) and thus have a patchy spatial distribution within the North Sea linked to habitat availability (Boulcott *et al.*, 2007). Adult sandeels (i.e. 1 year or older; 1+ group) spend the majority of the year submerged in the benthic substrate, only emerging in late winter to spawn, and in spring/early summer to feed on zooplankton, around the time of the plankton bloom (Winslade, 1971, 1974). Once laid, the eggs stick to sandy substrates until hatching around February or March (Macer, 1966; Wright and Bailey, 1996). Following this, sandeels display a planktonic larval stage, before metamorphosis into young of the year (0-group) fish at the start of summer, when they settle on sandy substrates. However, the strength and size of fish age classes is determined by food availability, along with predation, during the highly vulnerable period of larval development (Hjort, 1914; Cushing, 1990; Platt, Fuentes-Yaco and Frank, 2003). The dominant zooplankton in the region, *Calanus finmarchicus,* forms the major dietary component of sandeel, and is a critical factor determining North Sea sandeel recruitment (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009).

Sandeels are an important prey for many North Sea top predators, including seabirds, marine mammals and large predatory fish (Furness, 2002; MacLeod *et al.*, 2007; Engelhard *et al.*, 2013). The species also supports industrial fisheries in the region either directly, as stock, or indirectly, as prey for commercial species (Engelhard *et al.*, 2014). Thus, interannual variation in the availability of this key species can have important demographic consequences for higher trophic levels. For example, reduced sandeel availability has been suggested as a mechanism for reduced consumption of this species and concurrent increases in starvation mortality in harbour porpoises *Phocoena phocoena* (MacLeod *et al.*, 2007), while seabird breeding success is lower in the absence of this important prey (Monaghan *et al.*, 1989). Sandeels, like most abundant forage fish species in the region, display huge natural spatial and temporal variations in abundance, on both annual and decadal

time scales, but although this species is of critical ecological and economic importance, the exact mechanisms underlying these considerable fluctuations and their consequences for sandeel population dynamics remain poorly understood.

NORTH SEA ENVIRONMENTAL CHANGE

As one of the most rapidly warming marine ecosystems on the planet (Belkin, 2009), the North Sea is considered a "hot spot" for marine climate change impacts (Hobday and Pecl, 2014). Since the late 1980s there has been a sustained positive phase of the North Atlantic Oscillation index (Beaugrand, 2004), which is typically associated with warmer winter temperatures, stronger winds and increased amounts of oceanic inflow from the North Atlantic. As a result, the North Sea has warmed considerably over this period, increasing by 0.037°C yr^{-1} between 1982 and 2012 (Høyer & Karagali 2016). Consequent with this warming, regime shifts have been observed, along with alterations in the abundance, distribution and diversity of species in the region (Durant, Anker-Nilssen and Stenseth, 2003; Beaugrand, 2004; Perry *et al.*, 2005; Hiddink and ter Hofstede, 2008; Heath *et al.*, 2009).

One of the most important impacts of North Sea warming is its effect on zooplankton community composition, with a gradual shift from cold-temperate species towards those with warmer temperate affinities over the last half a century (Arnott and Ruxton, 2002; Beaugrand, 2004; Helaouët and Beaugrand, 2009; Frederiksen *et al.*, 2013). Of particular importance are reductions in *C. finimachus* abundance, the egg production of which peaks in March and is believed to be key to larval sandeel survival (Arnott and Ruxton, 2002). The increasing dominance of the later spawning *Calanus helogolandus* (Jónasdóttir *et al.*, 2005), has been suggested as a mechanism for reduced sandeel recruitment in response to ocean warming, due to trophic mismatch between *Calanus* egg availability and the highly vulnerable larval sandeel stages (van Deurs *et al.* 2009). Over the same period, substantial top-down fishing pressures have been exerted within the North Sea, including industrial extraction of both large predatory fish and sandeel (ICES 2008). Concurrently, several seabird populations in the region have exhibited substantial temporal variability in breeding success and dramatic population declines (Frederiksen, Wanless, *et al.*,

2004; Mitchell *et al.*, 2004; Frederiksen, Furness and Wanless, 2007), with changes in sandeel abundance and quality believed to be an important factor (Furness and Tasker, 2000; Wanless *et al.*, 2005; Frederiksen *et al.*, 2013; Cook *et al.*, 2014).

STUDY SYSTEM

The European shag *Phalacrocorax aristotelis* (hereafter shag), is a medium-sized seabird, endemic to the to the northeast Atlantic and Mediterranean coasts (Wanless and M. P. Harris, 1997). The UK supported 34% of the global shag population in 2000, but between 2000-15 the population declined by 34% (JNCC, 2016). Therefore, there is an urgent need to understand the relationships between North Sea environmental conditions, diet composition and demography in this rapidly declining, internationally important, shag population.

Shags breed colonially on rocky outcrops along the UK coast, raising between 1 and 4 chicks at a time and in exceptional circumstances can have two clutches in a year (Wanless & Harris 1997a; 1997b). Thus, shags have the capacity for rapid population growth under favourable environmental conditions, particularly if these conditions occur over successive years (Frederiksen *et al.*, 2008). Like other cormorants, shags have low body lipid stores and possess a partially waterproof plumage (Grémillet *et al.*, 1998), reducing buoyancy and allowing highly efficient underwater foraging (van Tets, 1976; Johnsgard, 1993; Wanless, Gremillet and Harris, 1998). However, such plumage, along with relatively few fat reserves, leaves shags vulnerable to the effects of inclement weather, when large numbers of birds can die due to hypothermia and/or starvation, in mass mortality events known as “wrecks” (Aebischer, 1986; Harris, Wanless and Elston, 1998; Frederiksen *et al.*, 2008). Reproduction can also be affected by inclement weather, either through direct effects on chick mortality, nest abandonment or impacts on breeding phenology (Potts, Coulson and Deans, 1980; Aebischer, 1993; Velando, Ortega-Ruano and Freire, 1999; Newell *et al.*, 2015). Thus, shags are unusual among seabirds in that they display both the capacity for rapid population growth and periodic population crashes, known as “boom-and-bust” population dynamics (Frederiksen *et al.*, 2008). Further, as long-lived organisms, shags may forgo breeding under poor

environmental conditions, leading to “non-breeding” events, where large number of birds defer reproduction (Aebischer and Wanless, 1992). Shags exhibit highly variable breeding phenology, which is related to a range of environmental conditions and intrinsic mechanisms, including SST, weather and age (Aebischer, 1993; Frederiksen, Harris, *et al.*, 2004; Daunt *et al.*, 2007). At the individual level reproductive output is strongly positively correlated with breeding date in shags (earlier breeding is more successful; Snow, 1960; Aebischer, 1993; Daunt *et al.*, 1999). At the population level this means that interannual variability in breeding phenology can have substantial impacts on reproductive output (Frederiksen, Harris, *et al.*, 2004). Shag diet is also relatively easy to quantify, as chicks occasionally regurgitate their last meal during routine handling at their nests when ringing chicks (Harris and Wanless, 1993). Further, full-grown birds regularly regurgitate indigestible prey remains in the form of pellets, which can be collected throughout the year at accessible locations, providing a rare opportunity to investigate diet outside of breeding (Lilliendahl and Solmundsson, 2006; Cosolo *et al.*, 2011). Owing to these highly variable and interlinked demographic traits, and the relative ease with which these can be quantified compared to most seabird species, shags provide an excellent system in which to test the impacts of environmental change and variability in the North Sea system on top predator demography.

Shags feed by foot-propelled, pursuit diving and predominantly forage within benthic habitats (Wanless & Harris 1997; Watanuki *et al.* 2008). Like many of the Phalacrocoracidae, shags are predominantly piscivorous, and as such, their diet has been the subject of substantial scientific investigation. Initially, this was due to the perceived impact of shag feeding on commercial fish stocks. For example, in the first published study on shags, Steven (1933) utilised a council-led cull to quantify the diet of shot birds, finding limited evidence of a conflict with fisheries. However, although shags in some populations do consume commercially important species, mainly Gadidae, the numbers exploited are likely to have limited impact on commercial fish stocks since the numbers consumed relative to that extracted by commercial fisheries is likely to be negligible (Hillersøy and Lorentsen, 2012). Instead, shags have been proposed as effective samplers of commercial fish stocks, in particular saithe

Pollachius virens (Barrett, 1991). For example, Bustnes *et al.* (2013) showed that shag breeding numbers are highly correlated with saithe *Pollacius virens* abundance estimates in Norway. Lorentsen *et al.* (2018) developed this idea further, showing that shag diet can be used as an early and reliable predictor of saithe recruitment, thereby providing a supplementary tool for adaptive fisheries management.

Due to highly flexible foraging habits, shag diet composition varies considerably throughout the species range (Barrett *et al.*, 1990; Swann, Harris and Aiton, 1991, 2008; Velando and Freire, 1999; Cosolo *et al.*, 2011; Hillersøy and Lorentsen, 2012; Bustnes *et al.*, 2013). For example, while sandeel is the dominant prey in many populations (Steven, 1933; Lumsden and Haddow, 1946; Pearson, 1968; Harris and Wanless, 1991, 1993), gadoids are important components in more northerly populations (Barrett *et al.*, 1990; Swann, Harris and Aiton, 1991, 2008; Velando and Freire, 1999; Cosolo *et al.*, 2011; Hillersøy and Lorentsen, 2012; Bustnes *et al.*, 2013) and in the Mediterranean a diverse prey base is exploited, including sand smelts *Atherina* spp., Bogue *Boops boops* and gobies (Velando and Freire, 1999; Cosolo *et al.*, 2011; Al-ismail *et al.*, 2013; Xirouchakis *et al.*, 2017). Seasonal variation in diet composition has also been recorded. For example, the diet of shags breeding in Galicia, Spain, changes from Gobidae and sand smelts *Athenna presbyter* in February and March, to sandeel in spring and early summer (Velando, Ortega-Ruano and Freire, 1999), while in Croatia, breeding shags consume a diverse range of bentho-pelagic prey, switching to Gobidae and other demersal prey during non-breeding (Cosolo *et al.*, 2011). In the Mor Braz Bay, France, Labridae and Gadidae dominate during breeding and non-breeding, respectively (Michelot *et al.*, 2017). As different prey species are associated with different habitats, changes in diet composition may also be associated with alterations in foraging habitats. Shags utilise a wide range of foraging habitats, including soft coral, rock, kelp forests and sand beds (Watanuki *et al.*, 2007, 2008), the relative usage of which can vary between the breeding and non-breeding period (Michelot *et al.*, 2017). However, long-term environmental change in the Northern Hemisphere may have had pronounced impacts on shag prey populations, foraging ability and demography. Such changes could have important implications for diet composition in this species,

yet no study has tested long-term trends in and the factors underpinnging shag diet composition over a range of spatial and temporal scales. Further, given that full-grown shags produce pellets, which can be collected throughout the year, this species may also provide a rare opportunity to quantify temporal trends in the year round diet of a marine top predator, which is also yet to be addressed.

The Isle of May (56°11'N, 2°33'W) is located within the mouth of the Firth of Forth, approximately 8 km from the mainland, on the south-east coast of Scotland (Figure 1). The island is elongate, running in a north-west to south-east axis (1.5km long by <500m wide; c.57 hectares) and is characterised by a rocky, low lying eastern coastline and contrasting west coast, dominated by high cliffs, the tallest of which is ~45m high. Designated as a National Nature Reserve and managed by Scottish Natural Heritage, the Isle of May is situated within the Forth Islands Special Protection Area. This island hosts internationally important numbers of breeding puffin, kittiwake, guillemot, razorbill *Alca torda*, and shag. Long-term monitoring of shags on the Isle of May started in 1963, initially through the ringing conducted by the Isle of May Bird Observatory. Since then, adult shags and unfledged chicks on the island have each been ringed with a unique, metal, alphanumerical British Trust for Ornithology ring (size K; EURING 800). More recently single (DARVIC) colour-rings, engraved with unique three letter identifying code, have also been applied. Intensive monitoring of puffin commenced in 1973 by the Centre for Ecology & Hydrology (formerly the Institute of Terrestrial Ecology), with the other species studied more intensively from the mid-1980s. As such, the Isle of May Long-Term Study provides one of the longest-running and comprehensive seabird demographic datasets in existence. Detailed information on shag demographic rates, including phenology, breeding success, diet and nest locations have been monitored throughout the island over this period and form the basis of this thesis.

Owing to this extensive monitoring, the shag population breeding on the Isle of May has been the subject of substantial scientific investigation over the past half a century (Aebischer, 1985, 1986, Harris and Wanless, 1991, 1993, 1996; Aebischer and Wanless, 1992; Aebischer, Potts and Coulson, 1995; Daunt *et al.*, 1999, 2001, 2007, 2014; Frederiksen, Harris, *et al.*, 2004; Watanuki *et al.*, 2008; Frederiksen *et al.*,

2008; Burthe *et al.*, 2012; Lewis *et al.*, 2015; Newell *et al.*, 2015). Over this period, the population has fluctuated markedly, initially increasing from 751 breeding pairs in 1965 to a maximum of 1916 pairs in 1987, before crashing from 1634 pairs in 1992 to 403 in 1994 and fluctuating thereafter (Figure 2). However, despite the substantial research on this population, there remains a limited understanding the demographic and dietary responses of this population to environmental change. In this thesis, I aim to explore the relationships between a suite of shag demographic parameters, environmental conditions and intrinsic factors, in order to develop further our understanding of the mechanisms underpinning population processes at this colony.

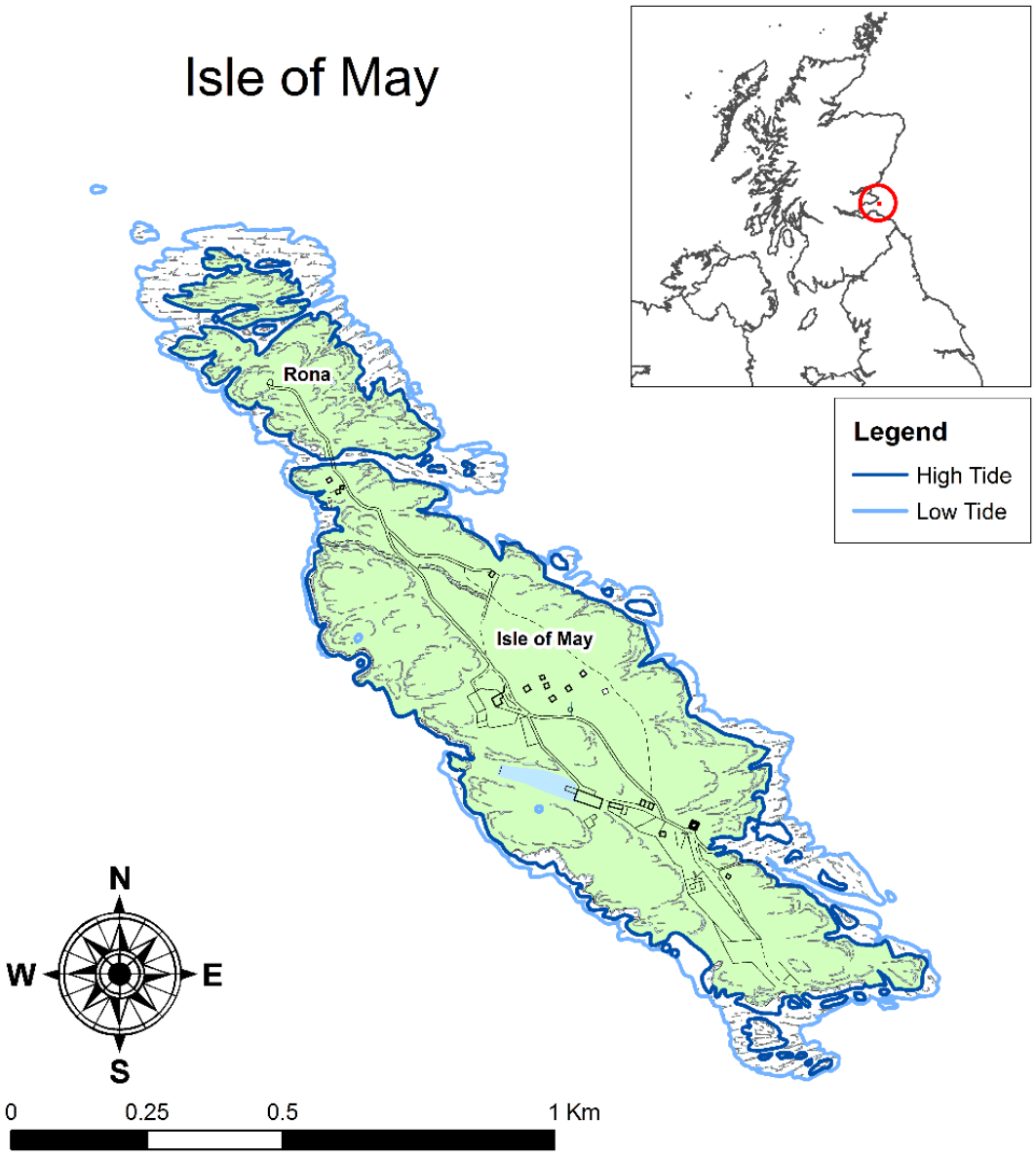

Figure 1 Map of the Isle of May displaying the high tide and low tide boundary. Red circle shows the location of the Isle of May, relative to the UK mainland. Map created using data from the EDINA Digimap® service (http://digimap.edina.ac.uk/roam/os).

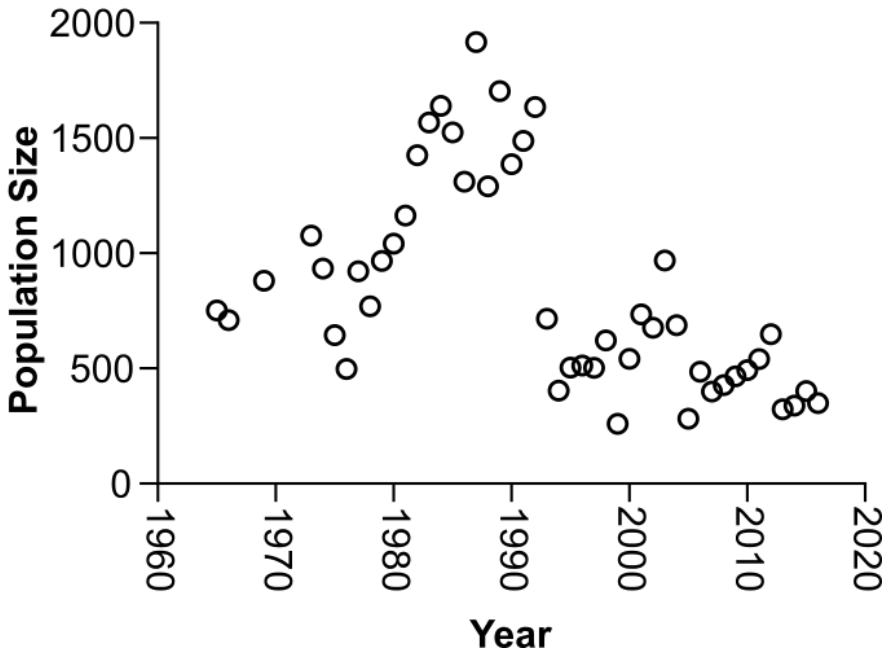

Figure 2 Interannual variation in breeding population size on the Isle of May between 1965 and 2016.

THESIS AIMS AND OUTLINE

The overall aim of this thesis is to utilise one of the longest running and comprehensive seabird datasets in existence, to test for long-term shag demographic trends and quantify the underlying environmental determinants in this rapidly changing marine environment. In **chapter 1,** I have provided an overview of environmental change, life-history theory, marine biology, seabird ecology and the North Sea study system. **Chapter 2** quantifies long-term trends in chick diet composition using regurgitated stomach contents collected at the nest between 1985 and 2014, and tests the underlying environmental determinants, over a range of temporal scales. The purpose of this study is to understand how changes in long-term mean climatic conditions and short-term weather variability may simultaneously affect the diet composition of marine predators. This chapter has been published in *Marine Ecology Progress Series*. Following on from this, **chapter 3** attempts to address the paucity of information regarding long-term trends in the year-round diet of full-grown seabirds. Using regurgitated pellets collected throughout the annual cycle between 1985 and 2014, I investigate whether long-term dietary trends differ between the breeding and non-breeding period. This information will allow us to better understand shag diet across the annual cycle, including which prey types are consumed during the energetically challenging winter months. This is a key knowledge gap in many species, as diet samples are difficult to obtain during this time. This chapter has been published in *Marine Biology*. **Chapter 4** tests for demographic trends and their drivers at this colony using data collected over half a century (1965-2016). The purpose of this analysis is to investigate whether climate-mediated and lagged effects operate directly on productivity or are mediated via phenology. This chapter is in preparation for submission to *Global Change Biology*. **Chapter 5** tests for long-term trends in fine-scale, within colony breeding distribution and the associated reproductive consequences on the Isle of May over 2 decades. This chapter is in preparation for submission to *Diversity and Distributions*. **Chapter 6** summarises the main findings, draws together each chapter, and identifies implications and priorities for future research.

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Chapter 2: From days to decades: short- and long-term variation in environmental conditions affect offspring diet composition of a marine top predator

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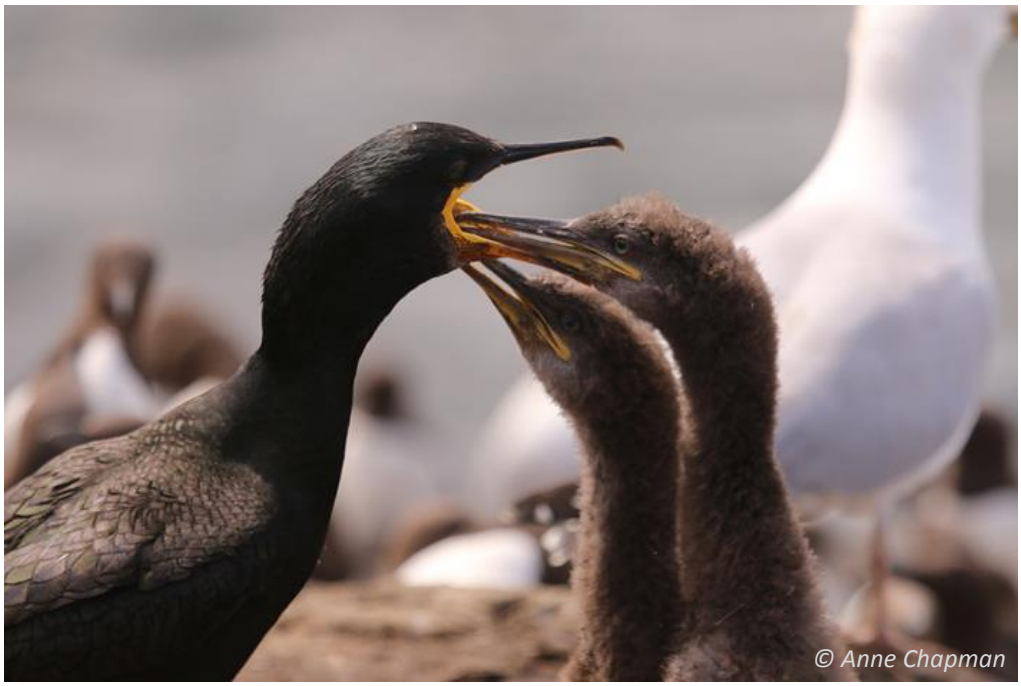

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ABSTRACT

Long-term changes in climate are affecting the abundance, distribution and phenology of species across all trophic levels. Short-term climate variability is also having a profound impact on species and trophic interactions. Crucially, species will experience long- and short-term variation simultaneously, and both are predicted to change, yet studies tend to focus on only one of these temporal scales. Apex predators are sensitive to long-term climate-driven changes in prey populations and short-term effects of weather on prey availability, both of which could result in changes of diet. We investigated temporal trends and effects of long- and short-term environmental variability on chick diet composition in a North Sea population of European shags *Phalacrocorax aristotelis* between 1985 and 2014. The proportion of their principal prey, lesser sandeel *Ammodytes marinus*, declined from 0.99 (1985) to 0.51 (2014), and estimated sandeel size declined from 104.5 to 92.0 mm. Concurrently, diet diversification increased from 1.32 to 11.05 prey types yr^{-1}, including members of the families Pholidae, Callionymidae and Gadidae. The relative proportion of adult to juvenile sandeel was greater following low Sea Surface Temperatures (SSTs) in the previous year. In contrast, the proportion of Pholidae and Prey Richness were higher following high SST in the previous year. Within a season, the proportion of sandeel in the diet was lower on days with higher wind speeds. Crucially, our results showed that diet diversification was linked to trends in SST. Thus, predicted changes in climate means and variability may have important implications for diet composition of European shags in the future, with potential consequences for population dynamics.

INTRODUCTION

The marine environment is changing rapidly, with profound ecological impacts observed across the globe (Poloczanska *et al.*, 2013). Much research has focused on the effects of mean temperature on the distribution, demography and phenology of marine animal populations, operating at annual and decadal temporal scales (Edwards and Richardson, 2004; Durant *et al.*, 2007; Sydeman *et al.*, 2015). There is also increasing evidence that shorter scale variability in climate linked to weather conditions can have dramatic fitness consequences (Boyce, Haridas and Lee, 2006). However, few studies have considered the effects of climate at multiple temporal scales on wild animal populations (Campbell *et al.*, 2012). Most climate models predict both an increase in mean temperature and the frequency and severity of extreme weather events in many regions (IPCC, 2014). Thus, to gain an understanding of how climate change may affect marine animal populations in future, it is important to quantify the effects of long- and short-term changes in environmental conditions simultaneously.

One of the principal mechanisms whereby climate can affect marine animal populations is through changes in the availability of resources, such as food. Long-term changes in resource availability may occur via alterations in primary production which propagate through food webs via bottom-up mechanisms (Hays, Richardson and Robinson, 2005; Perry *et al.*, 2005; Frederiksen *et al.*, 2006). In seasonal environments, climate change may also lead to spatial or temporal mismatch between resource demand and supply (Fretwell, 1972; Durant *et al.*, 2005; Grémillet *et al.*, 2008). Climate variability may also affect resource availability at shorter time scales, by directly altering abundance and distribution, or by affecting consumers' ability to forage (White, 2008). In many marine ecosystems, seabirds and other top predators often rely on a small number of prey species (Cury *et al.*, 2000). Top predators may respond to changes in the availability of these main prey within and between seasons by diversifying their diet, in line with optimal foraging theory (Stephens and Krebs, 1986). Such shifts may have important consequences for reproduction and survival, dependent on the relative availability and profitability of different prey.

A number of studies have demonstrated that long-term changes in the distribution, abundance and size of prey have led to changes in seabird diet (Miller and Sydeman, 2004; Gaston and Elliott, 2014; Green *et al.*, 2015). There is also evidence that seabird diet composition is altered by short-term weather conditions such as wind speed (Finney, Wanless and Harris, 1999; Stienen *et al.*, 2000; Elliott *et al.*, 2014), mediated by effects on flight performance and prey behaviour and catchability (Sagar and Sagar, 1989; Weimerskirch *et al.*, 2000; Lewis *et al.*, 2015; Kogure *et al.*, 2016). At intermediate temporal scales, diet composition may display seasonal patterns if alternative prey show different scheduling of key life-history events and associated availability (Lewis, *et al.* 2001a, Davoren & Montevecchi 2003). Such multi-scale temporal effects are important since diet composition is a key determinant of seabird demographic rates (Monaghan *et al.*, 1989; Reid and Croxall, 2001). The sensitivity of seabirds to these effects is particularly pronounced during the breeding season when individuals are faced with high energetic demands, the constraint of foraging close to the colony, and potentially high intra-specific competition for food linked to population density (Orians & Pearson 1979, Drent & Daan 1980, Birt *et al.* 1987, Lewis, *et al.* 2001b). However, to our knowledge, no study has simultaneously quantified the effects of daily, seasonal and interannual environmental conditions and breeding density on seabird breeding diet.

Here I use three decades of diet data from European shags *Phalacrocorax aristotelis* (hereafter shag) breeding at a North Sea colony, to quantify dietary trends and test associations with annual, seasonal and daily environmental conditions and annual breeding population density. The North Sea has warmed rapidly, increasing by 0.037°C yr^{-1} between 1982 and 2012 (Høyer and Karagali, 2016). Associated with this warming there have been marked changes on the abundance, distribution and phenology of many species at multiple trophic levels, including a switch in the dominant zooplankton species and a northwards shift in many fish species (Beaugrand, 2004; Perry *et al.*, 2005; Hiddink and ter Hofstede, 2008; Burthe *et al.*, 2012). Large parts of the North Sea exhibit a “wasp-waist” ecosystem (Cury *et al.*, 2000), characterised by high diversity at upper- and lower-trophic levels, but low diversity of mid-trophic species, dominated by a small planktivorous, shoaling fish,

the lesser sandeel *Ammodytes marinus* (hereafter sandeel). Sandeels have a clear annual cycle whereby spawning occurs in late winter, 1+ group (sandeels hatched prior to the current year) are active in the water column during spring (April/May) before burying in sandy sediments, while 0 group (young of the year) become available from June onwards following metamorphosis (Wright & Bailey 1996). Some sandeel populations have shown a decrease in abundance, size, growth rates, energetic quality and shifting phenology in recent decades linked to rising sea temperatures and associated changes in their copepod prey (Arnott and Ruxton, 2002; Wanless *et al.*, 2004; van Deurs *et al.*, 2009; Frederiksen *et al.*, 2011; Rindorf *et al.*, 2016). The sandeel is the principal prey of many top predators, including the majority of seabirds in the region (Furness and Tasker, 2000) and dramatic declines in several seabird breeding populations have been attributed to reduced sandeel availability (Mitchell *et al.*, 2004; Daunt and Mitchell, 2013).

Previous analyses of shag diet from the early period of this study demonstrated that, during the breeding season, this population were sandeel specialists (Harris and Wanless, 1991, 1993; Daunt *et al.*, 2008). However, diet varies substantially across the species range, including large numbers of Gadidae and Gobiidae taken by some populations, suggesting that shags adopt a flexible foraging strategy to exploit available prey (Steven, 1933; Furness, 1982; Cosolo *et al.*, 2011; Hillersøy and Lorentsen, 2012). Such flexibility could have resulted in a change in diet composition and diversity over the past three decades if sandeels have become scarcer and/or lessened in energetic value relative to alternative prey, or non-sandeel prey have become more common and/or increased in energetic value. Furthermore, although shags can extract sandeels from the sand (Watanuki *et al.*, 2008), they can achieve high profitability from pelagic shoals of 0 group sandeel when they become available late in the season (Wanless *et al.* 1998). Thus, a seasonal shift to 0 group might be expected, in line with Black-legged kittiwakes *Rissa tridactyla*, Atlantic puffins *Fratercula arctica* and common guillemots *Uria aalge* breeding at the same colony (Lewis *et al.* 2001a; Wanless *et al.* 2004; Daunt *et al.* 2008) . In addition, foraging and flight performance of shags is affected by daily wind conditions (Daunt *et al.*, 2006, 2014; Lewis *et al.*, 2015; Kogure *et al.*, 2016). Accordingly, short-term

weather may be important in determining shag diet composition if wind affects catchability or availability of different prey. Finally, the study population has declined from 1524 pairs in 1985 to 338 pairs in 2014, which may have affected diet composition through changes in intra-specific competition. Therefore, this population provides an excellent study system to test the dietary response of a top predator to interannual, seasonal and daily variability in environmental conditions and population density.

My specific aims were to:

a) test whether the mean annual proportion of sandeel in the diet and mean length of sandeels (an index of energetic value) has changed over the last thirty years and, if so, whether diet diversity has increased;
b) quantify whether diet composition is related to annual indices of prey availability (sea surface temperature and copepod abundance);
c) test whether there is a seasonal pattern in diet composition such that the proportion of 0 group sandeels is higher later in the season;
d) quantify the relationship between short-term weather conditions and diet composition; and
e) investigate the extent to which density of conspecifics is a determinant of annual diet composition.

METHODS

QUANTIFYING DIET

The study was conducted between 1985 and 2014 on the Isle of May National Nature Reserve, Firth of Forth, southeast Scotland (56°11‘N, 02°33’W). Diet was quantified during the chick-rearing period (April–July) in each year using a standardised methodology (Harris & Wanless 1991). During routine fieldwork, chicks and adults occasionally regurgitated food. Regurgitates were collected, visually inspected by experienced observers to determine the approximate proportional prey composition, weighed, and then frozen. Previous work has shown that food regurgitated by adults at the nest is predominantly destined for the brood (Wanless,

Harris and Russell, 1993), so I assumed that adult samples represented chick diet and pooled them with chick samples in the analysis (chick: n = 727 ; adult: n = 112; unknown n = 24).

Samples were subsequently thawed then placed in a saturated solution of biological washing powder (Biotex©) and heated at 40-50^{o}C for a minimum of five hours, until all soft tissue was digested. The residual hard parts (e.g. fish otoliths, vertebrae and mouth parts, Cephalopod beaks, and crustacea exoskeletons) were then identified to the lowest possible taxon using keys in Härkönen (1986) and Watt *et al.* (1997). Some items were identified to species level, but this was not possible in most cases. Therefore, fish prey were grouped by family, and molluscs, annelids and arthropods, which together contributed little to the diet (3% combined biomass over all years), by phylum. Otoliths were counted, and measured under a binocular microscope (25x magnification). Sandeels *Ammodytes* spp. (virtually all those identified were lesser sandeel *A. marinus* so hereafter sandeels refer to this species) were aged as 0 group or 1+ group using otolith macrostructure (ICES, 1995). The biomass proportion of each fish prey type in each regurgitate was calculated by converting otolith lengths into fish weights in two steps. First, fish lengths were estimated from relationships with otolith length. For 0 group and 1+ group sandeels, regression equations were used based on an annual sample of intact fish collected by mist-netting Atlantic puffins *Fratercula arctica* at this colony over the same period European shag *Phalacrocorax aristotelis* (hereafter shag) diet was sampled (Lewis *et al.* 2001a, updated). For other species, published otolith length/fish length regression equations were used (Lewis *et al.* 2003; Table A1). Second, species-specific length/mass regression equations were used to calculate fish weight and, therefore, biomass proportion of each prey type in each sample (Lewis *et al.*, 2003; Appendix 1.1 Table A1). Where no bones were present following digestion, the initial visual assessments of biomass proportions were used. This approach was appropriate as there was very close accordance between these two methods in samples where both were available (r^2 of arcsine transformed proportions of sandeels to non-sandeels of sandeels to non-sandeels = 0.96; n = 185). Only mean annual biomass proportions were available for 1989 (earlier years were lost in a fire).

Dietary response variables

Quantifying diet from regurgitates may involve biases due to differential rates of digestion, egestion and detectability of different prey types (Barrett *et al.*, 2007). I focussed on analysing patterns of change and association with environmental covariates of relative proportions of different prey types, because such analyses are robust to such biases. However, analysing biomass proportions can lead to problems of interpretation, because a change in one type cannot readily be distinguished from an opposite change in the others. Interpretation is particularly challenging where a small number of prey types dominate, as in my study where 83% of the diet comprised two prey types. To overcome this I undertook analyses of the relative proportions of different pairs of prey types in a hierarchical manner. First, I calculated the proportion of all sandeels relative to all other prey. Next, I calculated the proportion of 1+ group relative to 0 group sandeel. Finally, for each non-sandeel prey type, I calculated the proportion relative to all other non-sandeel prey, since the non-sandeel component was not dominated by a small number of prey types. This calculation was possible with three non-sandeel prey types: Pholidae, Gadidae and Callionymidae. The remaining prey types (Cottidae, Pleuronectidae, Clupeidae, Labridae, Gobiidae, Zoarcidae, Annelida, Blenniidae, Mollusca, Arthropoda, Lotidae and Syngnathidae) were rare, representing <0.05 of mean biomass proportion across all years combined and hence were not analysed individually relative to other non-sandeel prey.

Diet diversity was quantified by calculating the number of prey types in each regurgitate sample, which I refer to as sample-level Prey Richness. As Prey Richness is a count, it will systematically be higher at the aggregate, annual level than sample level (sample level Prey Richness range = 1-7; annual Prey Richness range = 1-12), so I considered both sample level and annual level Prey Richness (i.e. pooling information from all samples in each year). As with diet proportions, I analysed trends and environmental drivers of Prey Richness, which I considered robust to any biases associated with differential probability of presence in different prey types in regurgitated samples.

ENVIRONMENTAL COVARIATES

ANNUAL SANDEEL PROXIES

As there are no long-term abundance data for the local sandeel population upon which Isle of May shags feed, I utilised three environmental proxies of sandeel availability.

Sea Surface Temperature (hereafter SST): SST affects sandeel recruitment, via the bottom-up effects of temperature on the availability of key copepod prey (Wright and Bailey, 1993; Arnott and Ruxton, 2002; van Deurs *et al.*, 2009). Monthly SST data were obtained from the German 'Bundesamt fur Seeschiffart und Hydrographie' (http://www.bsh.de). Following Frederiksen *et al.* (2004), I calculated the mean of February and March SST for an inshore area surrounding the Isle of May (bounded by c. 56°0'N and 56°4'N, and 2°7'W and 2°3'W), overlapping with the summer foraging range of this population (Bogdanova *et al.*, 2014).

Calanus abundance: calanoid copepods, in particular the eggs and nauplii of *Calanus finmarchicus*, are of key importance to survival probability of early life stages of sandeels (Macer, 1966; Arnott and Ruxton, 2002; van Deurs *et al.*, 2009). I analysed 1597 samples from the Continuous Plankton Recorder (see Reid *et al.* 2003 for an overview) taken from a bounding box surrounding the Isle of May (55°N to 58°N, 3°W to 0°E), between 1984 - 2014. This box is larger than the summer foraging range of the study population, but ensured there were sufficient data for the analysis. I included two measures of *Calanus*: *C. finmarchicus* (stages V-VI) abundance (as a proxy for *C. finmarchicus* egg production; van Deurs *et al.* 2009) and *Calanus* nauplii abundance (for all species combined, as species-specific abundances were unavailable). For each measure, I calculated mean monthly abundance from February to May, since these months constitute the principal period of larval sandeel feeding (Wright and Bailey, 1996; van Deurs *et al.*, 2009).

Lagged covariates: the abundance of 1+ group sandeels is dependent on conditions experienced as 0 group fish in the previous year (Arnott and Ruxton, 2002). I therefore considered SST, *C. finmarchicus* (stages V-VI) abundance and

Calanus nauplii abundance lagged by one year as indices of the abundance of 1+ sandeel in the current year.

SEASONAL PREY AVAILABILITY

1+ group sandeels are active in the water column each spring, while 0 group sandeel become available in early summer following metamorphosis (Macer, 1966; Winslade, 1974; Wright and Bailey, 1993). I therefore tested whether there was a seasonal trend in diet composition from 1+ to 0 group sandeel by including the date of sample collection in analyses, which I refer to hereafter as day of year.

DAILY CONDITIONS

The flight and diving performance of shags is affected by local weather, in particular wind conditions (Daunt *et al.* 2006, Lewis *et al.* 2015, Kogure *et al.* 2016) and potentially rainfall, which in turn may affect diet composition, as previously shown in other seabirds (Finney, Wanless and Harris, 1999; Stienen *et al.*, 2000). Therefore, I used hourly wind speed (ms^{-1}) and daily rain (mm) data obtained from Leuchars Weather Station (56°23'N, 2°52'W), c.28 km from the study site (http:// badc.nerc.ac.uk), to calculate mean daily wind speed (ms^{-1}) and total daily rainfall (mm) on the day of sample collection.

POPULATION DENSITY

To account for potential density dependent effects, I fitted annual breeding population size, estimated using standardised protocols (Walsh *et al.* 1995).

STATISTICAL ANALYSIS

DIET TRENDS

All statistical analyses were conducted using R programming software (R Development Core Team, 2016) with figures created using the *ggplot2* package (Wickham, 2016) Trends in sample-level biomass proportions and Prey Richness were tested using Generalised Linear Mixed Models (hereafter GLMMs) fitted using the Penalized Quasi Likelihood methods in the *glmmPQL* function (*MASS* package, Venables & Ripley 2002), which automatically accounts for overdispersion. This method was chosen due to irresolvable model convergence issues relating to analysis of the sample-level diet data encountered using the *glmer* function in the *lme4*

package (Bates *et al.*, 2015). However, information-theoretic approaches, such as the *Akaike Information Criterion*, are not available using *glmmPQL*, hence model selection was conducted via backwards stepwise deletion. Binomial and Poisson models with a logit- and log-link link function, respectively, were fitted for biomass proportions and Prey Richness, respectively. I subtracted 1 from Prey Richness, to improve the plausibility of the assumption that the variable has a Poisson distribution. However, model results and plots are presented on the original, unadjusted scale. In each analysis, the fixed effect of year was centred on zero (by subtracting mean year from each value) and rescaled (by dividing the centred value by the standard deviation of year). Visual inspection of the data suggested that diet trends may have been non-linear, so I fitted a linear and quadratic effect of year. To account for repeat sampling, I fitted a categorical, random effect of year.

To identify trends in annual Prey Richness, where there was one estimate per year, I fitted a GLMM with a Poisson error family using the *glmer* function, subtracting 1 from each value. In this instance model selection was conducted using the Akaike's Information Criterion corrected for small sample sizes (hereafter AICc), with the best supported model considered to be the one with the lowest AICc, unless others were within two AICc, in which case they were considered to have equal support (Burnham and Anderson, 2002). A global model, containing both a linear and quadratic numeric fixed effect of year, was fitted to investigate trends along with a categorical, random effect of year to account for overdispersion. In addition, I weighted each annual Prey Richness value by the number of samples per year and included a fixed effect of log(number of samples year^{-1}) to account for any systematic change in Prey Richness with annual sample size.

Linear Mixed Effects Models (hereafter LMMs) were fitted to individual estimated fish length using the *lmer* function in the *lme4* package, with model selection conducted using AICc. Estimated fish length was only available from 1989 to 2014 and could only be modelled for 1+ and 0 group sandeel, as other prey occurred too infrequently in the first half of the study. I fitted year, age class and a year by age class interaction as fixed effects to test whether any trend in estimated length varied with age class, and a categorical, random effect of year to account for

repeat sampling. The *dredge* function in the *MuMIn* package (1.15-6, Bartoń 2016) was used to identify the best supported model for both annual Prey Richness and estimated fish length, based on AICc.

ENVIRONMENTAL COVARIATES

Effects of the environmental covariates (annual measures of SST, SST in t-1, *Calanus* nauplii abundance, *Calanus* nauplii abundance in t-1, *C. finmarchicus* abundance and *C. finmarchicus* abundance in t-1, day of year, Mean daily wind, Total daily rain, and Breeding population size) on sample-level biomass proportions and Prey Richness were quantified using GLMMs in the *glmmPQL* function. This analysis was selected because of the same irresolvable model convergence issues experienced in the analysis of trends in these variables. I had no biological *a priori* reason to test for interaction terms and therefore our analysis considered main effects only. To test for collinearity between covariates, I calculated Pearson's Correlation Coefficients. None were strongly collinear (max coefficient = 0.45; Appendix 1.2 Table A2) and hence all covariates were retained in the modelling process. A global model was fitted containing all potential fixed effects and a random, categorical effect of year, and model selection was the same as for the trends analysis of biomass proportions and sample-level Prey Richness.

Previous analyses have identified trends in environmental parameters within the North Sea (Burthe *et al.*, 2012), and the co-occurrence of trends in both dependent and independent variables may lead to spurious results (Grosbois *et al.*, 2008). Accordingly, I calculated Pearson's Correlation coefficients and associated p-values between all of the covariates and numeric year, and found temporal trends in some of the explanatory covariates (see results). Therefore, as a supplementary analysis I fitted year into the final dietary response models as a numeric fixed effect to remove any temporal effects in the response variable, and re-ran the model selection. Year was retained in the final model for all analyses, irrespective of whether a significant effect was found. The resulting models ('detrended models') were compared to the models without detrending ('non-detrended models'). I cannot exclude the possibility that where variables were only significant in non-detrended models, the effect was due to a correlation with a third variable that is

also showing a trend over time, and such relationships were therefore treated with caution. The results from the non detrended models are given in the main text and those from the detrended models in the Supplementary Material (Appendix 1.3 Table A3).

RESULTS

DIET COMPOSITION

A total of 863 diet samples were collected between 1985 and 2014 (n= 29 years; median: 26 samples year^{-1}; range: 4-69; n = 425 sample days; median: 14 days year^{-1}; range: 2-16; median day of year: 182; range: 82-228). Sixteen prey types were recorded, the commonest being sandeel *Ammodytes marinus* (hereafter sandeel) which represented 0.83 ± 0.35 (mean ± SD) of total biomass and occurred in 88% of samples (Table 1). 1+ group and 0 group sandeels contributed 0.70 ± 0.42 and 0.12 ± 0.30 respectively of total biomass, and occurred in 78% and 25% of samples, respectively. Other prey included Pholidae (0.05 ± 0.19 of total biomass, 8% of samples), Gadidae (0.04 ± 0.17; 9%), Callionymidae (Dragonets; 0.02 ± 0.17; 5%) and Cottidae (0.02 ± 0.09; 2%). Clupeidae, Pleuronectidae, Labridae, Zoarcidae, Gobiidae, Annelida, Arthropoda, Mollusca, Blenniidae, Lotidae and Syngnathidae each contributed 0.01 ± 0.10 or less of total biomass, with 0.01 ± 0.10 of the total biomass unidentifiable (Table 1). Overall, the estimated mean (± SD) length of sandeels was 101.10 ± 27.35 mm, with 1+ and 0 group sandeel 117.30 ± 13.46 mm and 74.74 ± 20.20 mm, respectively.

ANNUAL DIET TRENDS

The proportion of sandeel relative to all other prey types declined significantly over the study period, from 0.99 in 1985 to 0.51 in 2014 (Table 2, Figure 3a; Appendix 1.4 Table A4). However, there was no change in the relative proportion of 1+ group to 0 group sandeel (Table 2, Figure 3a; Table A4). There was no trend in the proportion of Pholidae or Gadidae relative to other non-sandeel prey (Table 2, Figure 3b; Table A4), but Callionymidae showed a significant decrease in the proportion relative to other non-sandeel prey from 0.57 in 1985 to 0.02 in 2014 (Table 2, Figure 3b). There was a

significant linear increase in sample-level Prey Richness from 1.03 in 1985 to 1.50 in 2014 (Table 2, Table A4). There was also a marked linear increase in annual Prey Richness from 1.32 in 1985 to 11.05 in 2014 (Table 3, Figure 4). There was no evidence of a quadratic relationship in the trends in biomass proportions, sample-level Prey Richness or annual Prey Richness (Table S3, Table A4).

Estimated mean length of sandeels declined by 12% over the study period, from 104.5 mm in 1989 to 92.0 mm in 2014 (Table 4, Figure 5). There was an interaction between year and age class, such that the decline in estimated length was more marked in 0 group sandeel (22.6% decline from 87.1 mm in 1989 to 67.4 mm in 2014) than 1+ group sandeel (4.5 % decline from 121.9 mm in 1989 to 116.4 mm in 2014; Table 4, Figure 5).

Table 1 Mean biomass proportion (± SD), number and percentage of samplesfor each prey class pooled over the entire study. Range of pooled annual mean values presented. The sum of 1+ and 0 group sandeel is less than total sandeel since 1% could not be aged.

Prey	Biomass ± SD	Range	Samples (%)
Sandeel (mainly *Ammodytes marinus*)	0.83 ± 0.35	0.28-1.00	734 (88%)
1+ group sandeel	0.70 ± 0.42	0.01-1.00	650 (78%)
0 group sandeel	0.12 ± 0.30	<0.01-0.94	211 (25%)
Pholidae (Gunnels)	0.05 ± 0.19	<0.01-0.40	69 (8%)
Gadidae (Cod fishes)	0.04 ± 0.17	<0.01-0.27	79 (9%)
Callionymidae (Dragonets)	0.02 ± 0.12	<0.01-0.08	18 (2%)
Cottidae (Cottids)	0.02 ± 0.09	<0.01-0.22	39 (5%)
Unidentifiable prey	0.01 ± 0.10	<0.01-0.12	16 (2%)
Pleuronectidae (Right-eyed Flounders)	0.01 ± 0.08	<0.01-0.08	28 (3%)
Clupeidae (mainly Herring and Sprat)	0.01 ± 0.08	<0.01-0.20	35 (4%)
Labridae (Wrasses)	<0.01 ± 0.06	<0.01-0.04	14 (2%)
Gobiidae (Gobies)	<0.01± 0.04	<0.01-0.06	19 (2%)
Zoarcidae (Eelpouts)	<0.01 ± 0.04	<0.01-0.03	6 (1%)
Annelida (mainly Polychaete worms)	<0.01 ± 0.02	<0.01-0.03	6 (1%)
Blenniidae (Blennies)	<0.01± 0.01	<0.01-0.02	2 (<1%)
Mollusca (Molluscs)	<0.01 ± 0.01	<0.01-0.01	17 (2%)
Arthropoda (mainly Crustacea)	<0.01 ± 0.01	<0.01-0.01	20 (2%)
Lotidae (Rocklings)	<0.01± 0.01	<0.01-0.01	4 (<1%)
Syngnathidae (Pipefishes)	<0.01	<0.01-<0.01	5 (1%)

Table 2 Estimates (± SE), t-value (t) and p-value (p) for linear trends in diet proportions. Year was standardized and values presented are on the logit scale.

Response variable	Est	SE	t	p
Sandeel relative to non-sandeel prey	-14.49	3.22	-4.50	<0.001
1+ relative to 0 group sandeel	4.65	5.42	0.86	0.398
Pholidae relative to other non-sandeel prey	5.48	4.17	1.31	0.202
Callionymidae relative to other non-sandeel prey	-13.91	4.84	-2.87	0.008
Gadidae relative to other non-sandeel prey	-0.10	4.69	-0.02	0.984
Sample-level Prey Richness	12.09	2.37	5.09	<0.001

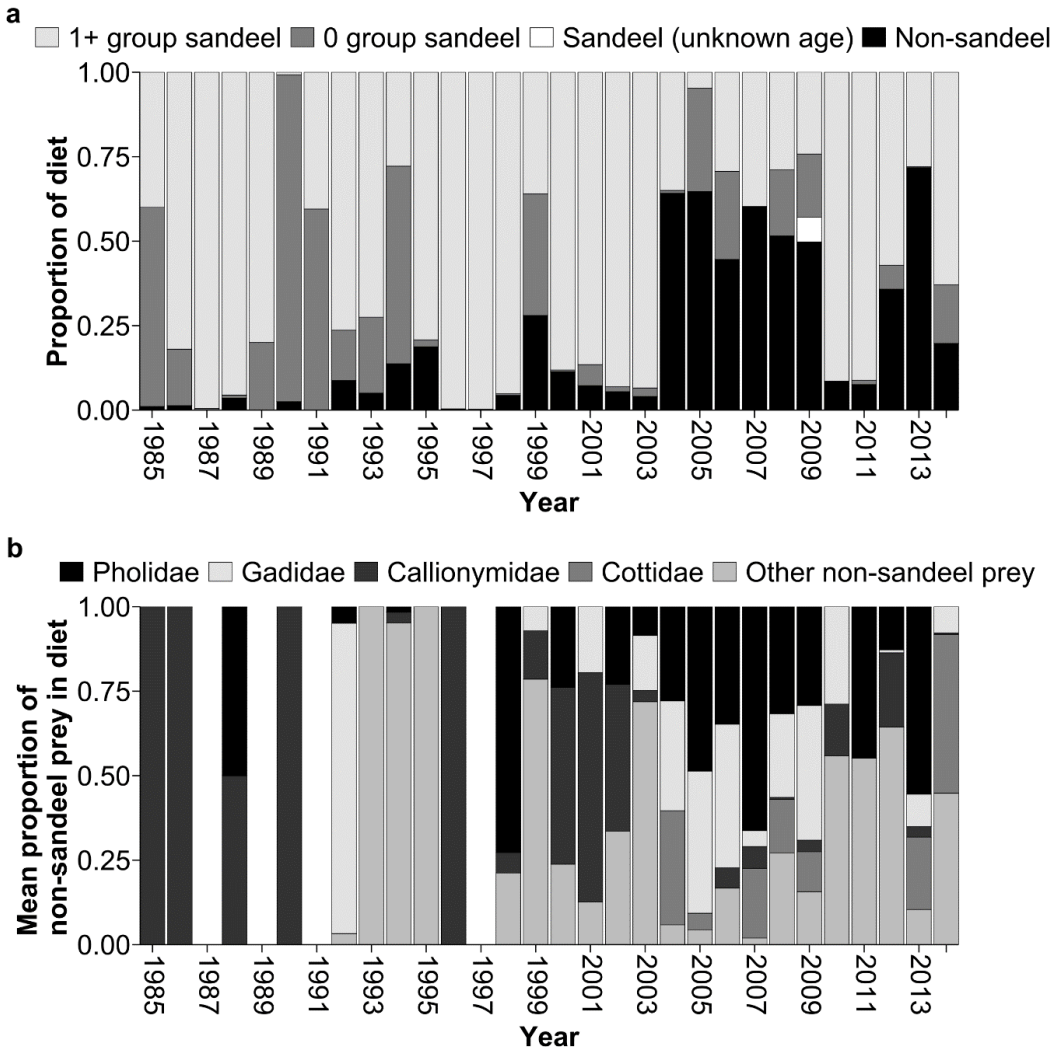

Figure 3 a) Interannual variation in biomass proportion (mean across samples in each year) of sandeel by age class and non-sandeel prey in the diet from 1985 to 2014. b). Interannual variation in biomass proportion (mean relative to all non-sandeel prey in each year) of non-sandeel prey in the diet from 1985 to 2014. Sandeel contributed 100% of the diet in 1987, 1989, 1991 and 1997.

Table 3 Model selection table for annual Prey Richness (GLMM), fitted with a log(number nests year^{-1}) offset. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z values, number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ω_i). *i* = intercept. "log(sample)" indicates that the log (sample number) in each year was included in each model as a fixed effect. Best supported models are highlighted in **bold**.

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
Annual Prey Richness	**1**	***Year***				**3**	**0.00**	**0.78**
		Year	**1.63**	**0.49**	**3.32**			
	2	*Year + Year^2*				4	2.82	0.19
		Year	1.64	0.49	3.33			
		Year^2	-0.19	0.54	-0.35			
	3	*i*				2	6.67	0.03

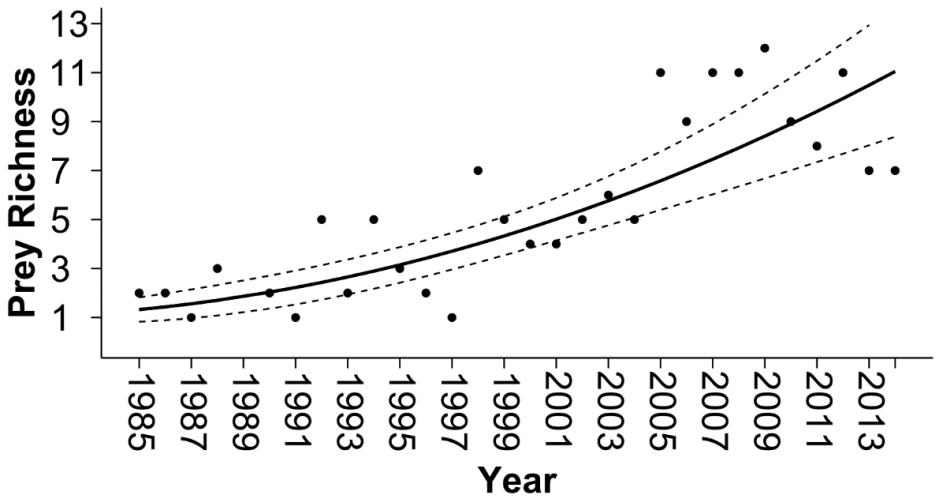

Figure 4 Interannual variation in annual level dietary Prey Richness from 1985 to 2014. Fitted line (±95 % CI) shows linear relationship on the log(expected value), which when plotted on the untransformed count data appears as a cubic relationship due to the Poisson distribution of the data.

Table 4 Model selection for sandeel length (LMM). Model structure, Fixed Effects, Estimates (±SE), t-value(t), Number of parameters (k), Akaike's Information Criterion corrected for small sample sizes (AICc), difference in AICc compared to top model (ΔAICc) and AICc Weight relative to other models (ωi), are displayed. i = intercept. Age class values are presented relative to the 1+ group category. Best supported models are highlighted in **bold**.

Response	Rank	Model	Est	SE	t	k	ΔAICc	ωi
Sandeel length	**1**	***Year + Age Class + Year * Age Class***				**5**	**0.00**	**1.00**
		Year	**-5.33**	**1.85**	**-2.89**			
		Age Class (1+ group)	**41.81**	**0.47**	**89.8**			
		Year * Age Class (1+ group)	**3.84**	**0.44**	**8.72**			
	2	*Year + Age Class*				4	73.60	<0.01
		Year	-3.53	1.76	-2.00			
		Age Class (1+ group)	42.65	0.46	93.34			
	3	*Age Class*				3	75.34	<0.01
		Age Class (1+ group)	42.64	0.46	93.27			
	4	*i*				2	6328.10	<0.01
	5	*Year*				3	6329.90	<0.01
		Year	-1.37	3.48	-0.39			

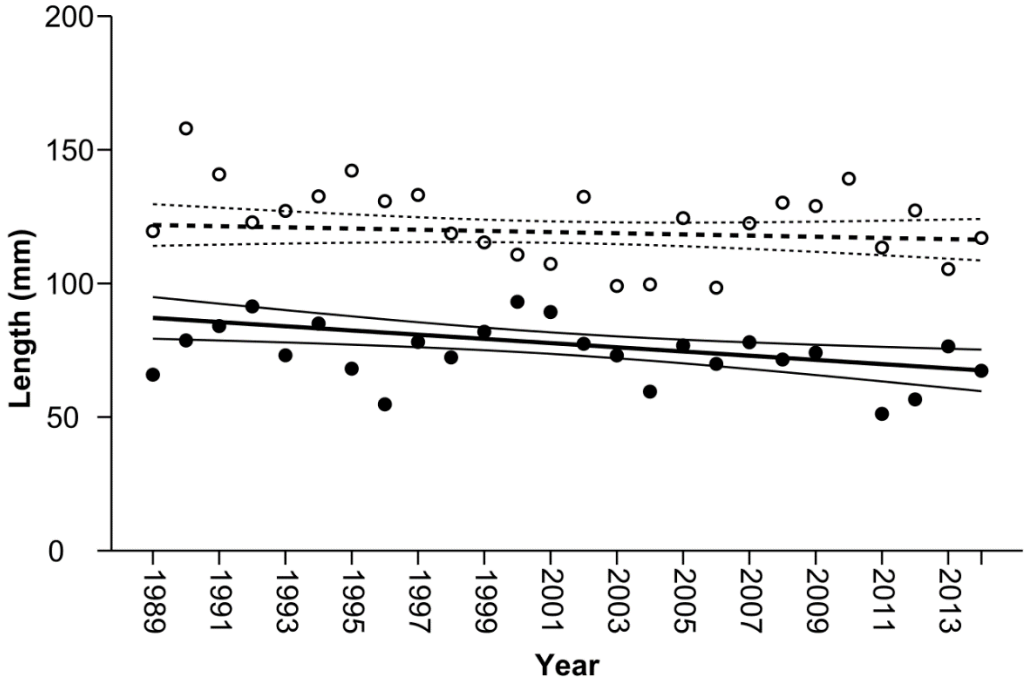

Figure 5 Interannual variation in sandeel length for 1+ group (○) and 0 group (●) sandeel from 1989 to 2014. Solid lines indicate the fitted line and confidence intervals for 0 group sandeel. Dashed line indicates the fitted line and confidence intervals for 1+ group sandeel. Analysis was conducted on individual fish length data (predicted from otoliths), but here I present annual mean values for each age class. Data were not available from 1985 to 1988 because records were lost in a fire.

Environmental Covariates

Over the study period, SST and *Calanus* nauplii abundance increased significantly, *Calanus finmarchicus* abundance and European shag *Phalacrocorax aristotelis* breeding population size declined, and date of sample collection advanced (Table 5). Mean daily wind speed and rain did not show a trend over time (Table 5).

Table 5 Pearson's correlation coefficients (r) and associated p-values (p) for correlations between explanatory covariates and year. Mean ± SD, maximum and minimum values displayed for each variable.

Covariate	Mean	Min	Max	r	p
SST	5.8 ± 0.6	4.5	6.8	0.44	<0.001
Calanus nauplii abundance	17 ± 15	0	55	0.14	<0.001
C. finmarchicus abundance	4 ± 4	0	19	-0.12	<0.001
Day of year	180 ± 20	82	228	-0.50	<0.001
Total daily rain (mm)	3 ± 6	0	51	-0.01	0.864
Mean daily wind (ms^{-1})	8 ± 3	2	24	0.06	0.078
Breeding population size	786 ± 494	259	1916	-0.73	<0.001

Annual Effects

The proportion of 1+ group relative to 0 group sandeel was higher when SST in February and March the previous year was lower (1.00 at 4.5°C vs 0.67 at 6.8°C). This decrease was relatively constant until ca. 6°C, the proportion of 1+ group dropped rapidly when temperature was higher (Table 6, Figure 6a). A greater proportion of Pholidae relative to other non-sandeel prey was associated with higher SST in the previous year, with a relatively steep, but consistent increase from 0.04 at 4.9°C to 0.57 at 6.8°C (Table 6, Figure 6b). Sample-level Prey Richness increased with SST in the previous year, from 1.05 at 4.5°C to 1.35 at 6.8°C (Table 6, Figure 7a). Years with higher abundance of *C. finmarchicus* were associated with a lower proportion of Pholidae (Table 6, Figure 6c). The proportion of Callionymidae in the diet relative to other non-sandeel prey was greater when the abundance of *Calanus* nauplii, both in the current and preceding year, was higher (Table 6, Figure 6d, Figure 6e). Years with a high abundance of *Calanus* nauplii were associated with a reduction in Prey Richness (Table 6, Figure 7b). None of the fixed effects were significant determinants

of the proportion of Gadidae in the diet relative to other non-sandeel prey. No other annual effects were significant.

SEASONAL AND DAILY EFFECTS

There was a seasonal decline in the proportion of 1+ group relative to 0 group sandeel, from a predicted value of 1.00 in March to 0.24 by August, driven by a sharp decline at the start of July (Table 6, Figure 6f). Furthermore, the proportion of sandeel relative to other prey types was lower on windier days (0.92 at 2 ms^{-1} vs 0.75 at 24 ms^{-1}; Table 6, Figure 6g). No other daily or seasonal effects were significant.

POPULATION DENSITY EFFECTS

The proportion of sandeel relative to other prey was greater when the breeding population size was larger, from a predicted value of 0.99 at 1916 pairs to 0.67 at 259 pairs (Table 6, Figure 6h). Furthermore, higher breeding population size was associated with an increase in Callionymidae in the diet, ranging from 0.48 at 1634 pairs to 0.03 at 259 pairs (Table 6, Figure 6i). Sample-level Prey Richness was also lower at higher breeding population sizes, ranging from a predicted value of 1.27 at 201 pairs to 1.03 at 1916 pairs (Table 6, Figure 7c). However, the detrending analysis removed the effect of population size from all analyses and thus this effect should be treated with caution (Supplementary Material Table S4).

Table 6 Response variables and fixed effects included in the final models of sample-level biomass proportions and Prey Richness in relation to environmental covariates. Estimates (±SE), t- and p-values are reported. t-1 indicates that covariates are lagged by one year. No fixed effects were found to be significant for the Gadidae model.

Response	Fixed effect	Est	SE	t	p
Sandeel relative to all non-sandeel prey	*Mean daily wind speed (ms^{-1})*	-0.06	0.03	-2.20	0.028
	Breeding population size	<0.01	<0.01	3.78	<0.001
1+ relative to 0 group sandeel	*Day of year*	-0.09	0.01	-7.38	<0.001
	SST t-1	-2.06	0.69	-2.98	0.006
Pholidae relative to other non-sandeel prey	*SST t-1*	1.73	0.44	3.95	<0.001
	C. finmarchicus abundance	-0.24	0.09	3.95	0.011
Callionymidae relative to other non-sandeel prey	*Calanus nauplii abundance*	0.05	0.02	3.44	0.002
	Calanus nauplii abundance t-1	0.05	0.02	3.14	0.005
	Breeding population size	<0.01	<0.01	3.11	0.005
Sample-level Prey Richness	*SST t-1*	0.97	0.34	2.85	0.009
	Calanus nauplii abundance	-0.03	0.01	-2.20	0.037
	Breeding population size	-<0.01	<0.01	-3.03	0.005

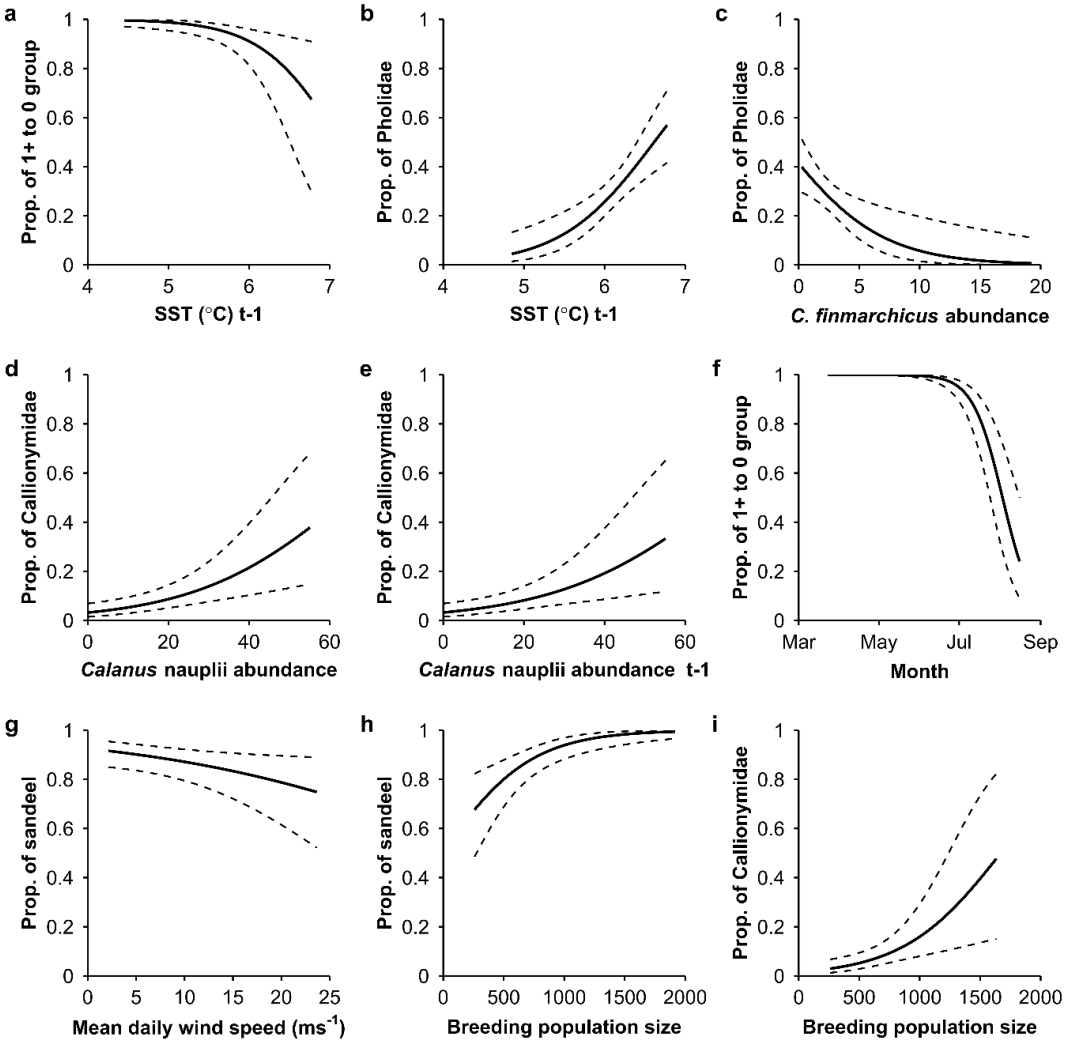

Figure 6 Fitted lines (±95 % CI) for probability of each of the modelled prey types occurring in the diet in relation to significant fixed effects in the final models. Proportion of 1+ relative to 0 group sandeel prey in relation to (a) Sea Surface Temperature (°C) in the previous year; proportion of Pholidae relative to non-sandeel prey in relation to (b) Sea Surface Temperature (°C) in the previous year and (c) mean spring C. finmarchicus abundance month^{-1} in the current year; proportion of Callionymidae relative to non-sandeel prey in relation to (d) mean spring *Calanus* nauplii abundance. month^{-1} in the current year and (e) mean spring *Calanus* nauplii abundance month^{-1} in the preceding year; proportion of 1+ relative to 0 group sandeel prey in relation to (f) day of year (presented as Month to aid interpretation); proportion of sandeel relative to all prey in relation to (g) mean daily wind speed (ms^{-1}) and (h) breeding population size; and proportion of Callionymidae relative to all non-sandeel prey relative to (i) breeding population size. Values are only displayed over the range for which data were included in the model. Predictions were made using Binomial GLMMs and setting additional fixed effects at the mean value. t-1 indicates that effects are lagged by one year.

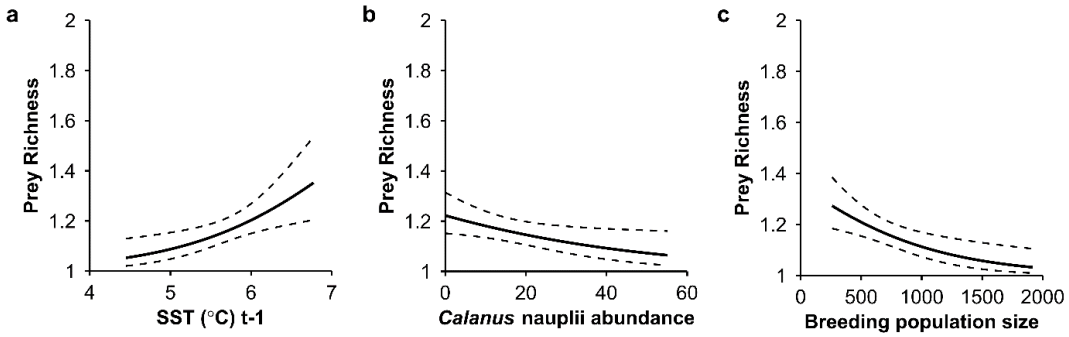

Figure 7 Fitted lines (±95 % CI) for sample-level Prey Richness in relation to significant fixed effects in the final model: (a) Sea Surface Temperature (°C) in the previous year, (b) mean spring *Calanus* nauplii abundance month-1 in the current year, and (c) breeding population size. Values are only displayed over the range for which data were included in the model. Predictions were made using Poisson GLMMs and by setting additional fixed effects at the mean value. t-1 indicates that effects are lagged by one year.

DISCUSSION

Using a data set spanning three decades, I quantified long-term dietary trends and tested the effects of environmental conditions on diet composition at interannual, seasonal and daily temporal scales. I found a marked reduction in the proportion of lesser sandeel *Ammodytes marinus* (hereafter sandeel) and a concurrent prey diversification over the study period, with a much wider range of prey items now exploited. I also identified a reduction in the size of both 1+ and 0 group sandeel in the diet. Overall, the diet showed both immediate and lagged responses to a suite of environmental conditions operating over a range of temporal scales, from days to decades. Furthermore, our results suggest that diet diversification over time was linked to the trend in SST in my study system. Thus, the predicted increases in climatic mean and variability at higher latitudes may lead to a further gerneralism in European shag *Phalacrocorax aristotelis* (hereafter shag) diet in future.

ANNUAL DIET TRENDS

Until the early 2000s, shags on the Isle of May fed their young mainly sandeels (Harris and Wanless, 1991, 1993; Daunt *et al.*, 2008), but chick diet has changed substantially over the last 15 years, with a decline in the main prey, sandeel, and an increase in diet diversity. Theory suggests that diet diversifies when predominant prey become

scarce and/or lessen in profitability (Stephens and Krebs, 1986), and empirical evidence in other seabird studies supports this (Croxall, Reid and Prince, 1999; Cosolo et al., 2011; Gaston and Elliott, 2014). Shags exploit a wide range of prey (Barrett, 1991; Velando and Freire, 1999; Lilliendahl and Solmundsson, 2006; Cosolo *et al.*, 2011; Michelot *et al.*, 2017) and can adjust their foraging behaviour in response to a change in availability of different prey types within their foraging range (Wanless, Gremillet and Harris, 1998; Daunt *et al.*, 2007; Bogdanova *et al.*, 2014; Michelot *et al.*, 2017). Changes in the availability of sandeels, non-sandeels or both may have contributed to the diet shift in my study population since many fish species have experienced changes in abundance and distribution in the North Sea, linked to ocean warming (Perry *et al.*, 2005; Heath *et al.*, 2012). However, this is challenging to investigate in detail in the absence of independent prey abundance data. The decline in estimated sandeel length may also have been a contributory factor underpinning the diet shift, since length is an index of energetic value (Hislop, Harris and Smith, 1991). This trend is in line with wider evidence of climate-mediated changes in the quality of sandeel in North Sea aggregations over the past three decades (Wanless *et al.* 2004, van Deurs *et al.* 2014). In particular, the decline of inshore sandeel aggregations fed on by shags mirror those recorded in offshore aggregations targeted by Atlantic puffins *Fratercula arctica* breeding on the Isle of May (Wanless *et al.*, 2004; Harris and Wanless, 2011). However, it is not possible to compare the extent of the change in fish length of inshore and offshore sandeels quantitatively, because lengths in puffin diet are measured from intact fish whereas those from shags are estimated from otolith length-fish length regression equations derived from sandeels in the diet of puffins. The parallel decline of sandeels and Callionymidae in shag diet may suggest a common environmental driver: the two likely species in the latter family, the common dragonet *Callionymus lyra* and the spotted dragonet *C. maculatus*, are associated with sandy habitats in common with sandeels (Heessen *et al.* 2015). In addition, Callionymidae may be encountered more frequently by chance when shags are searching for sandeels, and vice versa, leading to covariance in dietary proportions.

Environmental Covariates

ANNUAL EFFECTS

There was a negative relationship between the proportion of 1+ group relative to 0 group sandeel and SST in the previous year. Sandeel recruitment is strongly dependent on temperature, mediated by changes to key zooplankton prey species, in particular *Calanus finmarchicus* (Arnott & Ruxton 2002; van Deurs *et al.* 2009). Thus, this relationship suggests that temperatures in the previous year affect the abundance, size or quality of 1+ group in the current year (van Deurs *et al.* 2009) and, in turn, shag diet. The proportion of Pholidae relative to other non-sandeel prey was greater following warmer SST in the previous year. The Pholidae prey class contained solely the rock butterfish or gunnel *Pholis gunnellus* (hereafter butterfish), which are primarily associated with rocky and other coarse habitats (Shorty and Gannon, 2013). In Iceland, butterfish are larger in warmer water (Gunnarsson and Gunnarsson, 2002), and, in fish in general, the timing of egg hatching is inversely related to temperature, which hastens development (Pauly and Pullin, 1988). Earlier hatching in warmer years may thus extend the period of larval growth, increasing butterfish size and therefore profitability of this prey type for shags in the following year (Gunnarsson and Gunnarsson, 2002). Such physiological processes will not be unique to butterfish, but my patterns indicate that these may be overridden in other prey by factors such as food limitation. My results suggest that the opposite effects of temperature on proportion of 1+ group sandeel and Pholidae were independent, rather than a change in the abundance or availability of one type leading to a reciprocal dietary increase in the other. The positive effect of lagged SST on Prey Richness suggests that the abundance of 1+ group sandeel is reduced by higher temperatures in the preceding year, leading to diet diversification. Similar responses have been observed in other seabirds (Gaston and Elliott, 2014) which further supports the theory that in species with plastic foraging strategies, diet diversifies when the dominant prey becomes scarce or unprofitable in particular environmental conditions (Stephens and Krebs, 1986). Despite the increasing trend over time in SST, there was no trend in the relative proportions of different sandeel age classes or the proportion of Pholidae relative to other non-sandeel prey, two of the diet variables

affected by SST. However, there was an increasing trend in the third variable associated with SST, Prey Richness, which suggests that temperature was an important driver of diet diversification in this population, and may be related to previously reported increases in the diversity of available prey (Hiddink & ter Hofstede 2008).

Unexpectedly, no effect of either of the *Calanus* abundance measures was found on proportion of sandeels in the diet. Perhaps inshore sandeel populations exploited by shags may have different scheduling of life history events or environmental determinants from other North Sea populations, upon which our choice of covariates was based (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009). Alternatively, these measures may not be reliable as annual proxies of sandeel abundance. I selected *C. finmarchicus* abundance as a proxy of egg production, since eggs and nauplii of this species are key prey of younger egg classes of sandeel (van Deurs *et al.* 2009). Thus, there are multiple intermediate steps connecting *C. finmarchicus* and sandeel abundance that may each serve to weaken the relationship between them. Our second measure (*Calanus* nauplii) may also not be a reliable index of sandeel abundance since it comprises all *Calanus* species combined, including a number of species, in particular those with a preference for warmer sea temperatures, that may not be important in the diet of sandeels (Beaugrand, 2004). The negative relationship between the proportion of Pholidae relative to non-sandeel prey and *C. finmarchicus* abundance suggests that other non-sandeel prey may increase in abundance, size or profitability in years of high *C. finmarchicus* abundance. The positive effect of *Calanus* nauplii abundance in the current and preceding year on the proportion of Callionymidae is in line with this. Callionymidae are opportunistic feeders so may utilise abundant *Calanus* nauplii when they are available (Griffin, Pearce and Handy, 2012). This link may also underpin the negative relationship between Prey Richness and *Calanus* nauplii, whereby good feeding conditions for Callionymidae may result in shags reducing the consumption of other non-sandeel prey, leading to lower diet diversity. However, the concurrent increase in *Calanus* nauplii abundance and decrease in the proportion of Callionymidae

suggests that the trend in Callionymidae is likely to have been caused by some other factor.

SEASONAL EFFECTS

I demonstrated a seasonal switch from 1+ group to 0 group sandeels in the diet. Such a pattern is likely to be related to the temporal availability of the different sandeel age classes, with 0 group becoming available in the water column in June as 1+ group return to the seabed following their active spring feeding phase (Wright and Bailey, 1993). This switch has previously been shown in other seabird species breeding in the region (Lewis, *et al.* 2001a, Wanless *et al.* 2004, Daunt *et al.* 2008). However, in contrast to these species, which shift to 0 group when they become available in June, shags switched to 0 group a month later. Shags can extract sandeel directly from the seabed so 1+ sandeel remain potentially available throughout the breeding season (Watanuki *et al.*, 2008). Thus, they may switch to 0 group sandeels when these have grown large enough or if their large pelagic shoals move close enough to the island to be more profitable than buried 1+ group (Wanless, Gremillet and Harris, 1998). Alternatively, the timing of metamorphosis of inshore 0 group sandeels may be later in inshore populations than those offshore, although currently I have no data to test this assertion. Although the date of sample collection became earlier over the study period, related to advances in population phenology (r_s = 0.66), this trend did not appear to influence the relative proportions of different sandeel age classes, which showed no trend over time. This advance in timing of breeding is also unlikely to have explained the decline in sandeels in the diet relative to non-sandeels, since there was no seasonal pattern in relative proportions of these two prey types.

DAILY EFFECTS

The lower proportion of sandeel in the diet at higher wind speeds supports other studies which have demonstrated that weather conditions alter diet composition in seabirds (Finney, Wanless and Harris, 1999; Stienen *et al.*, 2000; Elliott *et al.*, 2014). This relationship may be linked to wind effects on foraging or flight ability (Daunt *et al.*, 2006, 2014; Lewis *et al.*, 2015; Kogure *et al.*, 2016). Enhanced water turbidity during strong winds may alter sandeel availability or catchability (Dunn, 1973), while increased flight costs in windier conditions, as is evident in species with flapping flight

(Gabrielsen *et al.*, 1991), may lead to individuals selecting different habitats and associated prey. Alternatively, high wind speeds may increase the availability of non-sandeel prey, although the mechanisms are unknown. However, despite detecting a significant negative effect of daily wind speed on the proportion of sandeel in the diet, there was no evidence that average daily wind speeds during the breeding season changed over the course of the study, and therefore I do not think that weather conditions contributed to the long-term decline in importance of sandeels.

POPULATION DENSITY

Theory and empirical evidence suggests that population density during the breeding season has the potential to affect diet composition of seabirds since adults may experience high intraspecific competition leading to prey depletion, which may not be equal across prey types (Ashmole 1963, Birt *et al.* 1987, Lewis, *et al.* 2001b). Shags and other inshore species may be particularly susceptible to this effect because of their highly restricted foraging range in the breeding season (mean-maximum range $bird^{-1}$ in the Isle of May breeding population ± SE: 17.7 ± 8.4 km; Bogdanova *et al.* 2014). However, breeding population size, which declined markedly over the study period, was removed from all models in the detrending analysis, suggesting that other factors were more important in explaining the dietary trends.

CONSEQUENCES OF DIETARY CHANGE

Understanding the environmental determinants of diet composition over a range of temporal scales can provide important insights into the environmental causes of current and future change in seabird populations, since diet composition is a key determinant of seabird demography (Monaghan *et al.*, 1989; Reid and Croxall, 2001). Key metrics underpinning this link are prey capture rate, which integrates search and handling times, and energetic value. Variation in foraging efficiency associated with these measures may affect chick growth rates and adult body condition and, in turn, breeding success, post-fledging survival or adult survival (Olsson, 1997; Davis, Nager and Furness, 2005). Energy density appears similar between sandeels and the majority of alternative prey for which data exist (Spitz *et al.*, 2010). However, in order to investigate the potential consequences of the diet shift, locally estimated

energetic value (integrating prey size and energy density) and capture rates of different prey is a priority for future work. The diversification in diet means that shags now forage for prey associated with a broader range of habitats than they did at the start of the study period, including those associated with rocky habitats (Watanuki *et al.* 2008). Such changes may alter interactions with potential threats, such as small-scale offshore renewable developments. In 2000, the UK had 34% of the global population of European shags (Wanless and Harris, 2004), but by 2015 the UK population declined by 34% (JNCC, 2016). This is in line with similar declines observed in other sandeel dependent species, such as black-legged kittiwake *Rissa tridactyla* which declined by 44% over the same period (JNCC, 2016). Given predictions of an increase in climatic mean and variability in many regions (IPCC 2014), there may be further changes in shag diet. In particular, the link between SST and Prey Richness that I observed suggest that ocean warming may lead to further diet generalisation, while an increased frequency and severity of extreme wind events may further reduce the dietary contribution of sandeel. Such changes could have important consequences on future population dynamics in this species.

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Chapter 3: Pronounced long-term trends in year-round diet composition of the European shag *Phalacrocorax aristotelis*

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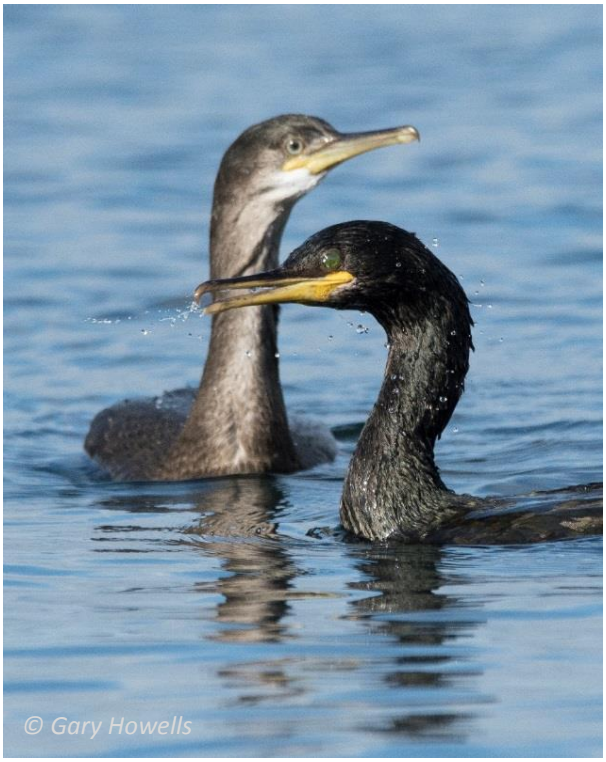

Author contributions: The study was conceived by RJH, FD, SJB, JAG, SW and MPH; data were collected and processed by SW, MPH, MAN, FD, SJB and DGJ, RJH did the analysis with advice from AB; RJH wrote the manuscript with input from all co-authors.

ABSTRACT

Populations of marine top predators are exhibiting pronounced demographic changes due to alterations in prey availability and quality. Changes in diet composition is a key potential mechanism whereby alterations in prey availability can affect predator demography. Studies of long-term trends in diet have focused on the breeding season. However, long-term changes in non-breeding season diet is an important knowledge gap, since this is generally the most critical period of the year for the demography of marine top predators. In this study, I analysed 495,239 otoliths from 5,888 regurgitated pellets collected throughout the annual cycle over three decades (1985–2014) from European shags *Phalacrocorax aristotelis* on the Isle of May, Scotland (56°11‘N, 02°33’W). I identified dramatic reductions in the frequency of lesser sandeel *Ammodytes marinus* occurrence over the study, which was more pronounced during the non-breeding period (96% in 1988 to 45% in 2014), than the breeding period (91% to 67%). The relative numerical abundance of sandeel per pellet also reduced markedly (100% to 13% of all otoliths), with similar trends apparent during breeding and non-breeding periods. In contrast, the frequencies of Gadidae, Cottidae, Pleuronectidae and Gobiidae all increased, resulting in a doubling in annual Prey Richness from 6 prey types per year in 1988 to 12 in 2014. This study demonstrates that the declining importance of the previously most prominent prey and marked increase in diet diversity is apparent throughout the annual cycle, suggesting that substantial temporal changes in prey populations have occurred, which may have important implications for seabird population dynamics.

INTRODUCTION

Marine environments are changing rapidly across the globe due to a range of anthropogenic activities, including pollution, overfishing and climate change (Halpern, 2009; Poloczanska *et al.*, 2013). These effects have altered the abundance and distribution of lower trophic organisms such as plankton, with consequences for mid-trophic level fish which are the principal prey for a guild of marine top predators (Cury *et al.*, 2000; Frederiksen *et al.*, 2006). Many marine top predator populations are declining markedly in association with these changes in prey availability and quality (Paleczny *et al.*, 2015; Sydeman *et al.*, 2015). Altered diet composition is a key potential mechanism whereby changes in prey availability can affect marine top predators (Reid and Croxall, 2001; Cury, Boyd, Bonhommeau, Anker-Nilssen, Robert J. M. Crawford, *et al.*, 2011). Several studies have demonstrated long-term changes in marine top predator diet, in particular seabirds (Miller and Sydeman, 2004; Gaston and Elliott, 2014). However, these studies have mainly been undertaken during restricted periods of the annual cycle, because of logistical challenges of obtaining diet data throughout the year. In seabirds, diet studies are usually conducted during the breeding season, from samples delivered by adults to offspring (Barrett *et al.* 2007). However, the non-breeding period is critically important for the population dynamics of seabirds, since most mortality occurs at this time (Weimerskirch, 2002; Frederiksen *et al.*, 2008). Thus, a key question in understanding the link between changes in prey availability and seabird population dynamics is the extent to which there have been long-term changes in non-breeding season diet, and whether these differ from those during the breeding season.

Our understanding of seabird diet outside the breeding period is largely based on indirect methods such as stable isotopes and fatty acid analysis (Owen *et al.*, 2013; Kowalczyk *et al.*, 2014) or samples from shot/dead birds (Blake, 1984; Harris *et al.*, 2015). Such studies have produced valuable insights into non-breeding diet, demonstrating marked differences from the breeding season, owing to a combination of altered prey availability (Kowalczyk *et al.*, 2015), energetic constraints (Markones, Dierschke and Garthe, 2010), habitat association (Ainley *et al.*, 1996) and, in migratory species, altered locations (Ronconi *et al.*, 2010). However,

there is very limited information on long-term changes in non-breeding diet. Green *et al.* (2015) examined differences in breeding and non-breeding season diet in Cape gannets *Morus capensis* over a thirty-year period. However, due to sporadic sampling, their trends analysis was restricted to the breeding period only. To my knowledge, no published studies have quantified long-term trends in non-breeding season diet composition in seabirds, and compared these with trends in breeding season diet from the same population.

In this chapter, I analysed three decades of year-round diet in the European shag *Phalacrocorax aristotelis* (hereafter shag) collected on the Isle of May, south-east Scotland. The shag is a coastally distributed seabird that spends a large proportion of the day and every night on land (Wanless and M. P. Harris, 1997). Full-grown shags regularly regurgitate pellets containing prey remains, which can be collected at accessible roosts, offering a rare opportunity to quantify year-round diet (Barrett *et al.*, 2007). Shags show a flexible foraging strategy such that diet varies substantially across the species range. Lesser sandeel *Ammodytes marinus* (hereafter sandeel) is the dominant prey in many populations (Harris and Wanless, 1993; Velando and Freire, 1999; Lilliendahl and Solmundsson, 2006), but at others, Gadoids (Gadidae), in particular saithe *Pollachius virens*, are the principal prey (Swann, Harris and Aiton, 2008; Lorentsen, Anker-Nilssen and Erikstad, 2018). Seasonal variation in diet composition has been recorded in some populations in response to changes in prey availability (Velando and Freire, 1999; Lilliendahl and Solmundsson, 2006). Previous studies of the Isle of May population demonstrated that, in the late 1980s and early 1990s, the diet of shags consisted mainly of sandeels, with limited evidence of seasonal differences in diet composition (Harris and Wanless 1991, 1993). However, the North Sea has warmed substantially over the past three decades (Høyer and Karagali, 2016), which has resulted in changes in the distribution, abundance and diversity of many fish populations, including sandeel (Perry *et al.*, 2005; van Deurs *et al.*, 2009; ter Hofstede, Hiddink and Rijnsdorp, 2010). In chapter 2, I demonstrated a marked decline in the proportion of sandeel in shag chick diet on the Isle of May, from 0.99 (1985) to 0.51 (2014), over this period, along with a concurrent dietary diversification. I attributed this dietary change to climate-

mediated alterations in the availability of sandeels and alternative prey. Similarly, a community-scale analysis of seabird breeding diet at this colony demonstrated a decline in the importance of sandeels over the past three decades (Wanless *et al.*, 2018). As local sandeel populations are resident (Boulcott *et al.*, 2007), it is probable that any effect of environmental change on abundance or quality of these populations will affect both breeding and non-breeding diet of shags which over-winter on the Isle of May. Thus, I predicted a decline in the importance of sandeel in the diet throughout the annual cycle. However, sandeel availability varies among seasons since they are present in the water column during the spring and summer, but are buried in the sand during the winter, apart from a brief period when they emerge to spawn (Wright and Bailey, 1993). Furthermore, environmental conditions, habitat use and energetic costs also vary between seasons (Daunt *et al.*, 2014; Michelot *et al.*, 2017). Thus, any changes in overall prey abundance or availability during the study might have different effects on diet composition at different times of the year. However, whether long-term changes in diet composition outside the breeding season has matched trends observed in diet during the breeding season (chapter 2) is untested. Therefore, my specific aims were to:

a) quantify year round diet composition of shags over three decades; and

b) test whether dietary trends differ between the non-breeding and breeding period.

METHODS

QUANTIFYING DIET

The study was conducted between 1985 and 2014 at a European shag *Phalacrocorax aristotelis* (hereafter shag) colony on the Isle of May National Nature Reserve, Firth of Forth, south-east Scotland (56°11‘N, 02°33’W). Shags are present on the island throughout the year, with a resident proportion of the breeding population joined in winter by migrants from other locations (Grist *et al.*, 2014), allowing for the collection of pellets throughout the year. Pellets were collected opportunistically (mean number of sample days $year^{-1}$ ± SD: 23 ± 14; range: 3–49) at roosts and breeding

colonies using forceps, placed into a plastic bag and frozen. The breeding status and age of individuals that produced pellets was unknown. However, as chicks do not produce pellets, all samples were from full-grown (i.e. fledged) birds (Russell, Wanless and Harris, 1995).

Samples were submerged in a saturated solution of biological washing powder (Biotex©) and heated at 40–50^{o}C, until all soft tissue and mucus was digested. Residual hard parts (e.g. fish otoliths, vertebrae and mouth parts, cephalapod beaks, mollusc shells and crustacea exoskeletons) were then identified to the lowest possible taxon using keys in Härkönen (1986) and Watt *et al.* (1997), allowing the presence/absence of each prey type to be recorded in each pellet. Sandeels *Ammodytes* spp. (principally, lesser sandeels *A. marinus*; Harris and Wanless 1991; hereafter refered to as sandeel), the most frequent prey type recorded, have previously been classified in dietary studies on the basis of age (Harris and Wanless, 1991; chapter 2). However, differentiating between sandeel age classes is generally not possible from otoliths obtained from pellets due to the effect of digestive erosion on otolith structure. Therefore, for the purposes of this study, all sandeels were aggregated into a single prey category. The presence of sand was also noted, since it may arise from accidental ingestion when foraging in sandy habitats and therefore be an index of prey species that live in these habitats, notably sandeels (Winslade, 1974; Holland *et al.*, 2005). The number of otoliths of each prey type in each pellet was then counted. Each fish has two otoliths, but due to the large numbers that may be encountered in a pellet and the potential for otoliths within a pair to undergo differential digestion, it was not possible to accurately match otoliths from the same fish. Therefore, each otolith was treated as an individual sample within each pellet.

Pellet analysis has been used to quantify diet in a range of seabirds, including shags, cormorants, skuas and terns (reviewed in Barrett *et al.* 2007). In appropriate study systems, large sample sizes may be obtained in a non-intrusive way throughout the year. However, quantifying diet from pellets involves two well-established limitations that must be considered when interpreting the data. First, due to differential rates of erosion, small or soft prey may be completely absent or under-

represented in pellets, with larger prey, or those with more resilient body parts, more commonly retained (Barrett *et al.* 2007). For example, Johnstone *et al.* (1990) showed that in captive shags the recovery of otoliths from Sprat *Sprattus sprattus*, sandeel and Cod *Gadus morhua* was 17%, 20% and 52%, respectively. Accordingly, the most robust diet metric used to quantify prey in pellets is frequency of occurrence, in which items are scored on the basis of presence or absence. This method does not capture prey types that are completely digested, but accounts for any differential in digestion rates among prey types that are recorded by giving equal weighting to prey types irrespective of abundance in the sample. I also considered a second diet measure that is typically quantified from pellets, the numerical abundance of different prey types. This measure is more informative, but must be interpreted with care because it is more sensitive to the effects of differential digestion rates (Barrett *et al.*, 2007).

A second limitation of quantifying diet from pellets is that the exact date when the prey were ingested is not known. However, the vast majority of pellets were fresh when collected, and they do not persist on rocks at the study colony because they disintegrate in rain or are consumed by herring gulls *Larus argentatus,* so I consider that pellets will have been produced within ca. two weeks of the sampling date.

DIETARY RESPONSE VARIABLES

For each pellet, I recorded the presence or absence of diagnostic remains (e.g. fish otolith, vertebra, bone, mollusc shell, cephalopod beak) of each prey type. Frequency of occurrence was then calculated as the percentage of pellets in which the prey type was found in each period within each study year. I focused my analysis on frequency of occurrence of the top five most abundant fish prey: sandeel *Ammodytes* spp., Gadidae (Cod Fishes), Cottidae (Cottids), Pleuronectidae (Flatfish) and Gobiidae (Gobies). All other prey types occurred in ≤ 10% of pellets and could thus not be analysed robustly, but due to their low prevalence in the diet, I consider the omission of these prey unlikely to significantly affect my interpretation of changes in diet composition.

Numerical abundance is typically quantified as the proportion of otoliths of a given fish prey type relative to all otoliths in the pellet. However, where the diet is dominated by a small number of prey types, as in this study (Sandeel 88% and Gadidae 7% of all otoliths), analysis of relative proportions leads to problems of interpretation, since a change in one prey type cannot be readily distinguished from a reciprocal change in the other. I therefore modelled number of sandeel otoliths relative to all prey otoliths and number of Gadidae otoliths relative to all non-sandeel prey otoliths. All other individual prey types occurred too infrequently for their relative abundance to be analysed. However, their summed contribution was < 5% of all otoliths.

Diet diversity was quantified by calculating sample-level Prey Richness, which was the number of prey types recorded in each pellet. Due to the effects of digestion on prey items, it was not generally possible to identify all body parts to species level, but to a higher taxonomic level which varied with prey type (fish: family; Crustacea and Mollusca: subphylum; Polychaeta: class). As Prey Richness is a count, the aggregate, annual Prey Richness (pooling all pellets in each year) was systematically higher than the sample average (sample-level Prey Richness: median: 5; range: 0–9; annual Prey Richness: median: 12; range: 6–14). However, as annual Prey Richness is a measure of the total number of prey types exploited each year, I included it in my analysis.

Defining breeding and non-breeding periods

For the purpose of this study, a study year commenced at the onset of breeding in one calendar year and ended at the commencement of breeding in the subsequent calendar year. To determine the timing of onset of breeding in each study year I calculated the month in which the population median egg laying date occurred, estimated from weekly observations at long-term monitoring plots (1985–2014: median day of year: range: 101–181; Newell *et al.* 2015; updated). In shags, average incubation duration of a clutch of three eggs, the modal clutch size in this population, is 36 days (Potts, Coulson and Deans, 1980), with fledging occurring at a mean of 53 days after hatching (range: 48–58, n = 35; Potts *et al.* 1980). Therefore, I defined each

breeding season as the month of median egg laying date plus the following three months. This four month period was longer than the breeding period of individual pairs (~3 months), but was designed to capture the spread of laying that occurs in each year (Daunt *et al.*, 2007). I found that 97% of all observations of breeding activity (defined as observations of incubating eggs or brooding chicks; n = 29,075) at the long-term monitoring plots occurred in this four month time window, confirming that it was a robust representation of the breeding period. The non-breeding period commenced in the first month after the breeding period until the last month before the month of median laying date in the following year (range of months: breeding: April–September; non-breeding: August–May; Appendix 2.1 Table A5).

Statistical analysis

All statistical analyses were conducted using the R programming software (R Development Core Team, 2016). To test for temporal trends and effects of period (breeding vs non-breeding) on sample-level presence, relative numerical abundance and Prey Richness, I fitted Generalised Linear Mixed Models (hereafter GLMMs), using the 'glmer' function in the 'lme4' package (Bates *et al.*, 2015). Binomial models with a logit-link function were fitted for presence and relative numerical abundance, and Poisson models with a log-link function for sample-level Prey Richness. For each of the sample-level dietary components I fitted a global model containing fixed effects of year, period and a year by period interaction. This framework allowed me to test for temporal trends, the differences between periods, and differing temporal trends between breeding and non-breeding periods in each of the dietary components. Within each model, I also included random effects for month, year and month nested within year, to account for residual temporal autocorrelation. To account for overdispersion, I also included an individual, sample-level random effect in models of sandeel otoliths relative to all prey and Gadidae relative to non-sandeel prey (Harrison, 2015). I did not consider sample date as an explanatory variable, since this variable had no clear biological relevance, due to the variable time elapsed between pellet production and collection.

To identify trends in annual Prey Richness, where there was just a single value per year, I fitted a Poisson GLMM with a log-link function. I subtracted 6 (the minimum annual Prey Richness value over the study) from each value, so that the data are consistent with the distributional properties of the Poisson distribution. However, I present the results and plots on the original, unadjusted scale. This step was not necessary with the sample-level Prey Richness data, as the minimum value was zero i.e. pellets where no species were identified. Visual inspection indicated that the annual Prey Richness may be exhibiting non-linear trends. To test this, a global model containing both a linear and quadratic numeric fixed effect of year was fitted, along with a categorical, annual level random effect of year to account for overdispersion (Harrison, 2015). I weighted each annual Prey Richness value by the number of pellets per year and included a fixed (offset) effect of log(number of pellets $year^{-1}$) to account for any systematic change in annual Prey Richness with annual sample size.

In order to compare models with different fixed effects but the same random structure I used maximum likelihood in all models (Zuur *et al.*, 2009). In each analysis, the fixed effect of year was centred on zero (by subtracting mean year from each value) and rescaled (by dividing the centred value by the standard deviation of year). The inclusion of all years in the analysis led to difficulties with model convergence. Preliminary analyses confirmed that this was caused by the inclusion of years where samples were not collected in both the breeding and non-breeding periods, so these were excluded from the modelling process (707 samples in 7 years; 1985–87, 1994, 1998–99, 2008).

Model selection was performed on the four models (null, year, period, and year by period interaction) for each variable using Akaike's Information Criterion corrected for small sample sizes (AICc), where the best-supported model was considered to have the lowest AICc value compared to alternative models. Models within two AICc ($\Delta AICc < 2$) of the top model were deemed as having similar levels of support (Burnham and Anderson, 2002), unless they contained an additional parameter, in which case they were considered uninformative (Arnold, 2010). Analysis was conducted according to an established protocol (Zuur, Ieno and Elphick,

2010), with the 'MuMIn' (Bartoń, 2016) package used to obtain model selection outputs (see Supplementary Material for full details of model selection). Due to the large number of models, I only report those within 10 AICc points of the best model in the main text.

For figures and tables, annual means were calculated by pooling all samples in each period within a year. For presence, each mean value was calculated as the frequency of occurrence i.e. the percentage of samples in which the prey class was present. For numerical abundance, each mean value was calculated as the proportion of all otoliths of a given prey type relative to all otoliths. To aid comparison with frequency of occurrence, I converted numerical abundance proportions into percentages. Study years commenced at the onset of breeding, so each spanned two calendar years. All study years were retained in figures of annual mean data (1985–2014), with model plots presented over the range of years included in the analysis (1988–2014).

RESULTS

PELLET COMPOSITION

A total of 5888 pellets were collected between 1985 and 2014 (n = 23 years; mean ± SD pellets year^{-1}: 256 ± 212; range: 31–973; Appendix 2.2 Table A5), with 5668 (96%) containing at least one identifiable prey type. The data set comprised 3140 pellets from the breeding period (mean ± SD pellets year^{-1}: 136 ± 112; range: 0–342) and 2,748 from the non-breeding period (mean ± SD pellets year^{-1}: 119 ± 132; range: 0–538; Appendix 2.3 Table A6).

Fifteen individual prey types were identified using all prey remains (Table 7). Fish were the dominant prey, with lesser sandeel *Ammodytes marinus* (*hereafter* sandeel), the most frequently encountered, occurring in 79% of pellets (Table 7; Figure 8a). The next most frequently encountered prey was Gadidae (Cod Fishes) occurring in 41% of pellets (Figure 8b), followed by Cottidae (Cottids; 20%; Figure 8c), Pleuronectidae (Righteye Flounders; 19%; Figure 8d) and Gobiidae (Gobies; 19%; Figure 8e). All other prey occurred in ≤ 10% of pellets (Table 7). Sand occurred in 52%

of pellets (Figure 8e; Table 7). The median sample-level and annual Prey Richness was 5 (range: 0–9) and 12 (range: 6–14), respectively.

Table 7 Summary table of frequency of occurrence of each prey type and sand between 1985-86 and 2014-15, including the % for all pellets combined, mean of annual % and range of annual %. Prey that could not be identified to any taxonomic level are referred to as Unidentified.

Prey	Pellets (%)	Annual Mean ± SD	Annual Range
Sandeel	4668 (79%)	77% ± 17	47–96%
Gadidae	2409 (41%)	46% ± 17	22–75%
Cottidae	1149 (20%)	21% ± 16	2–47%
Pleuronectidae	1145 (19%)	19% ± 9	4–33%
Gobiidae	1126 (19%)	22% ± 16	2–56%
Crustacea	585 (10%)	13% ± 7	2–27%
Callionymidae	414 (7%)	9% ± 9	0–25%
Pholidae	364 (6%)	7% ± 10	0–32%
Mollusca	354 (6%)	7% ± 8	0–26%
Zoarcidae	346 (6%)	8% ± 9	0–40%
Labridae	210 (4%)	5% ± 5	0–16%
Polychaeta	181 (3%)	4% ± 3	0–7%
Syngnathinae	50 (1%)	1% ± 3	0–15%
Clupeidae	23 (< 1%)	< 1% ± < 1	0–2%
Agonidae	7 (< 1%)	< 1% ± < 1	0–2%
Unidentified	366 (6%)	6% ± 7	0–30%
Sand	3070 (52%)	48% ± 22	12–84%

I recorded 495,239 otoliths belonging to 11 fish prey types, with 4913 (83%) pellets containing at least one identifiable otolith (Table 8; mean ± SD otoliths pellet^{-1}: 84 ± 117; range 0–1048). Otoliths were dominated by sandeel (88%; mean ± SD relative numerical abundance per sample: 70 ± 40%). Gadidae were the second most common (7%; mean ± SD: 46 ± 41% numerical abundance relative to all non-sandeel otoliths). All other fish prey comprised < 5% of otoliths (Table 8).

Table 8 Summary table of otolith numerical abundance for each fish prey type between 1985-86 and 2014-15, including total number of otoliths (and %), annual mean ± SD number of otoliths pellet^{-1}, and range of annual number of otoliths.

Prey	Otolith	Annual Mean ± SD	Annual Range
Sandeel	434,629 (88%)	62.63 ± 36.80	1081–97,665
Gadidae	33,897 (7%)	6.93 ± 5.60	139–5044
Gobiidae	9830 (2%)	1.17 ± 1.24	3–1098
Cottidae	6558 (1%)	2.05 ± 1.80	11–1500
Pleuronectidae	6291 (1%)	1.11 ± 0.86	2–737
Pholidae	1787 (< 1%)	0.29 ± 0.56	0–691
Zoarcidae	1031 (< 1%)	0.25 ± 0.40	0–262
Callionymidae	805 (< 1%)	0.17 ± 0.30	0–214
Labridae	335 (< 1%)	0.08 ± 0.09	0–64
Clupeidae	64 (< 1%)	0.01 ± 0.05	0–25
Agonidae	12 (< 1%)	<0.01 ± <0.01	0–5

Temporal and seasonal changes in pellet composition

The best-supported model for sandeel presence contained an effect of year, period and a year by period interaction (Table 9; full model selection table presented in Appendix 2.3 Table A7). Overall, sandeel frequency of occurrence decreased markedly in both the breeding and non-breeding periods. However, the decline was more pronounced during the non-breeding period, from 96% in 1988 to 45% in 2014, compared to 91% to 67% during the breeding season (data values: Figure 8a; predicted values from model: Figure 9a). The best-supported model for both Gadidae and Cottidae presence contained an effect of year only (Table 9; Table A7). Gadidae frequency of occurrence increased from 22% in 1988 to 66% in 2014 (data values: Figure 8b; predicted values from model: Figure 9b), whereas Cottidae frequency of occurrence increased from 5% in 1988 to 45% in 2014 (data values: Figure 8c; predicted values from model: Figure 9c; Table 9; Table A7). Overall, there was an increase in Pleuronectidae presence over the study, driven predominantly by the breeding period, when frequency of occurrence increased from 7% (1988) to 23% (2014), with frequency during the non-breeding period remaining relatively constant at 15% in 1988 and 14% in 2014 (data values: Figure 8d; predicted values from model: Figure 9d; Table 9; Table A7). Gobiidae presence increased overall between 1988 and

2014, but there was a significant interaction between year and period such that presence was higher during the non-breeding period at the start of the study (breeding 2%; non-breeding 6%), while by the end of the study the frequency was the same in both periods (breeding 21%; non-breeding 21%; data values: Figure 8e; predicted values from model: Figure 9e; Table 9; Table A7). Presence of sand displayed a substantial decline over the study, with a significant year by period interaction such that frequency reduced from 44% to 19% during breeding and 92% to 16% in the non-breeding period (data values: Figure 8f; predicted values from model: Figure 9f; Table 9; Table A7).

Sandeel numerical abundance relative to all otoliths decreased from 100% in 1988 to 13% in 2014, but there was no evidence of a difference between the breeding and non-breeding periods (data values: Figure 10a; predicted values from model: Figure 11a; Table 10; full model selection table presented in Appendix 2.4 Table A8). The decline was less marked at the start of the study, but accelerated from the early 2000s. Gadidae numerical abundance relative to all non-sandeel otoliths reduced overall, but was consistently higher during breeding (data values: Figure 10b; predicted values from model: Figure 11b; Table 10; Table A8). The magnitude of change was similar in the two seasons, from 68% (1988) to 48% (2014) in the breeding period, and from 54% (1988) to 34% (2014) in the non-breeding period.

Sample-level Prey Richness increased over the study, but with a more marked increase during breeding (from 1.16 prey types pellet^{-1} in 1988 to 3.36 in 2014) than non-breeding (1.67 prey types pellet^{-1} in 1988 to 2.69 in 2014; data values: Figure 12a; predicted values from model: Figure 13a; Table 11; full model selection table presented in Appendix Table A9). Annual Prey Richness displayed a quadratic trend over the study, increasing from 6.27 prey types year^{-1} in 1988 to 12.31 in 2014, with a peak of 15.80 in 2007 (data values: Figure 12b; predicted values from model: Figure 13b; Table 11; Appendix 2.5 Table A9). However, a model containing a linear effect of year received similar support, providing strong evidence for an increasing trend in annual Prey Richness.

Table 9 Model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on presence of each prey type. Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z ratios, number of parameters (k), difference in AICc between top model and selected model (Δ AICc) and Akaike weight relative to other models (ω_i). Due to the large number of prey types and models, I only report those models within 10 AICc points of the top model, which is shown in **bold** (for full model selection tables see Appendix 2.3 Table A7).

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
Sandeel	**1**	***Year + Period + Year*Period***				**5**	**0.00**	**1.00**
		Year	**-0.54**	**0.22**	**-2.42**			
		Period (NB)	**0.24**	**0.16**	**1.52**			
		Year* Period (NB)	**-0.64**	**0.15**	**-4.35**			
Gadidae	**1**	***Year***				**3**	**0.00**	**0.43**
		Year	**0.67**	**0.11**	**6.35**			
Gadidae	2	*Year + Period + Year*Period*				5	0.12	0.41
		Year	0.83	0.13	6.36			
		Period (NB)	0.02	0.18	0.1			
		*Year*Period (NB)*	-0.28	0.14	-1.99			
Gadidae	3	*Year + Period (NB)*				4	1.95	0.16
		Year	0.67	0.11	6.27			
		Period (NB)	0.04	0.19	0.24			
Gobiidae	**1**	***Year + Period + Year*Period***				**5**	**0.00**	**0.78**
		Year	**0.91**	**0.19**	**4.75**			
		Period (NB)	**0.7**	**0.26**	**2.69**			
		Year*Period (NB)	**-0.41**	**0.19**	**-2.16**			
Gobiidae	2	*Year + Period (NB)*				4	2.57	0.22
		Year	0.72	0.16	4.45			
		Period (NB)	0.84	0.25	3.33			
Pleuronec-tidae	**1**	***Year + Period + Year*Period***				**5**	**0.00**	**0.98**
		Year	**0.46**	**0.12**	**3.96**			
		Period (NB)	**0.23**	**0.21**	**1.1**			
		Year*Period (NB)	**-0.47**	**0.14**	**-3.33**			
Pleuronect-idae	2	*Year + Period (NB)*				4	8.96	0.01
		Year	0.23	0.1	2.36			
		Period (NB)	0.37	0.2	1.84			
Cottidae	**1**	***Year***				**3**	**0.00**	**0.64**
		Year	**0.92**	**0.14**	**6.62**			

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
Cottidae	2	*Year + Period*				4	2.00	0.24
		Year	0.92	0.14	6.62			
		Period (NB)	-0.01	0.19	-0.06			
Cottidae	3	*Year + Period + Year*Period*				5	3.30	0.12
		Year	0.98	0.16	6.27			
		Period (NB)	-<0.01	0.19	-0.01			
		*Year*Period (NB)*	-0.11	0.14	-0.84			
Sand	**1**	***Year + Period + Year*Period***				**5**	**0.00**	**1.00**
		Year	**-0.41**	**0.25**	**-1.66**			
		Period (NB)	**1.62**	**0.32**	**5.1**			
		Year*Period (NB)	**-1.01**	**0.25**	**-4.04**			

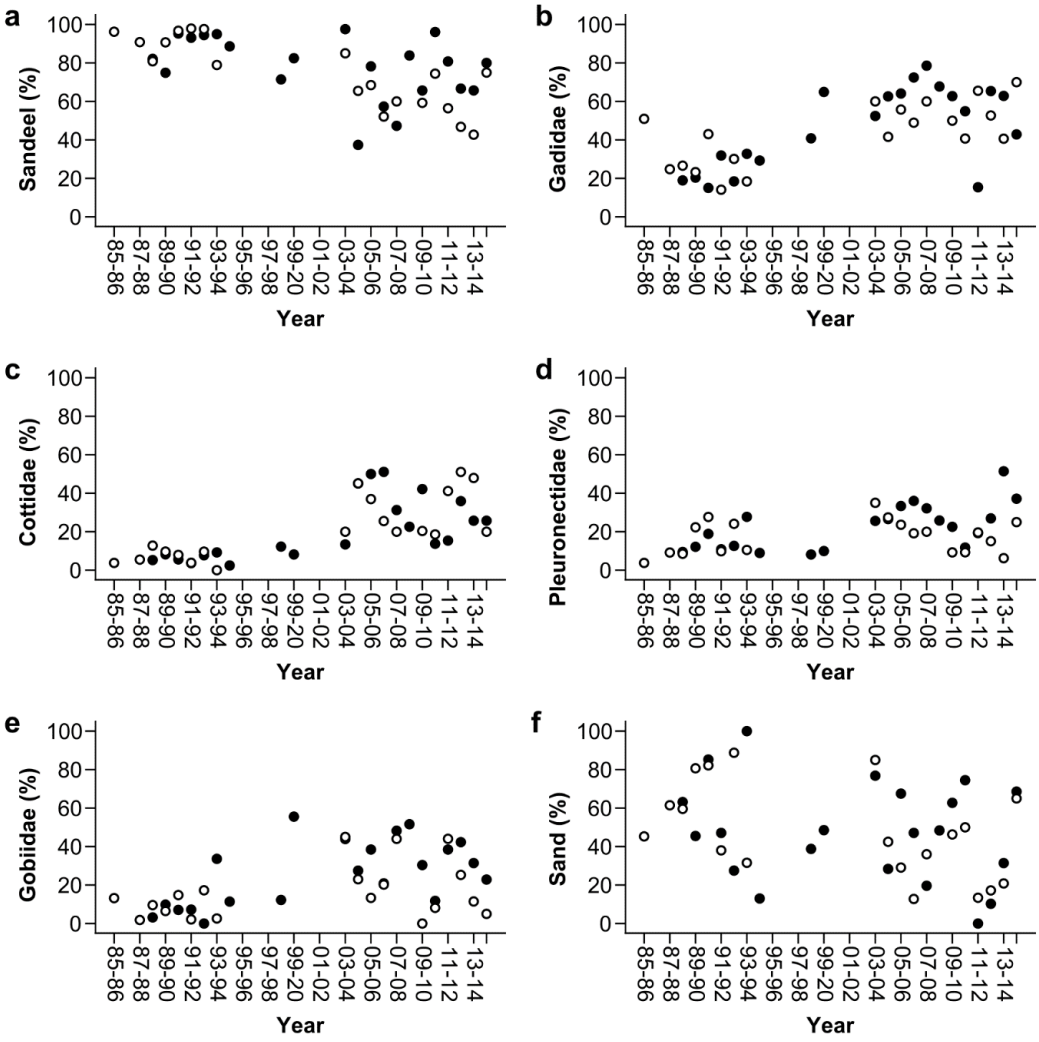

Figure 8 Interannual variation in breeding (●) and non-breeding (○) frequency of occurrence between 1985-86 and 2014-15 for: a) Sandeel; b) Gadidae; c) Cottidae; d) Pleuronectidae; e) Gobiidae; and f) Sand.

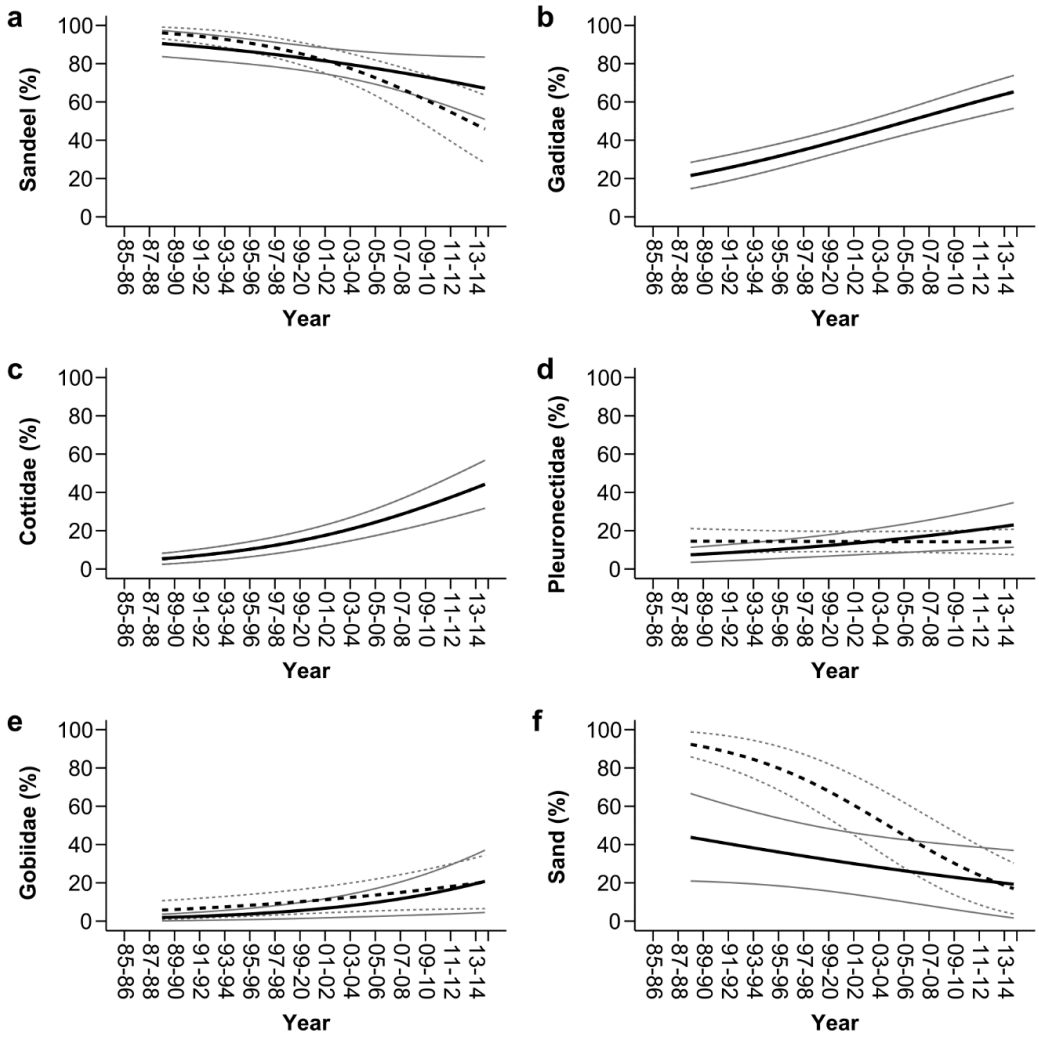

Figure 9. Fitted lines and 95% confidence intervals for frequency of occurrence between 1988-89 and 2014-15 for: a) Sandeel; b) Gadidae; c) Cottidae; d) Pleuronectidae; e) Gobiidae; and f) sand. Plots with a single line indicate a year effect only. Plots with two fitted lines indicate differences in trends between periods (breeding period: solid line; non-breeding period: dashed line).

Table 10 Model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on numerical abundance of sandeel (relative to all otoliths) and Gadidae (relative to all non-sandeel otoliths). Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z ratios, number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ω_i). Due to the large number of prey types and models, I only report those models within 10 AICc points of the top model, which is shown in **bold** (for full model selection tables see Appendix 2.4 Table A8).

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
Sandeel	**1**	***Year***				**3**	**0.00**	**0.65**
		Year	**-2.84**	**0.31**	**-9.03**			
Sandeel	2	*Year + Period*				4	1.89	0.25
		Year	-2.83	0.32	-8.87			
		Period (NB)	-0.14	0.39	-0.35			
Gadidae	**1**	***Year + Period***				**4**	**0.00**	**0.92**
		Year	**2.07**	**0.12**	**16.61**			
		Period (NB)	**-0.65**	**0.23**	**-2.79**			

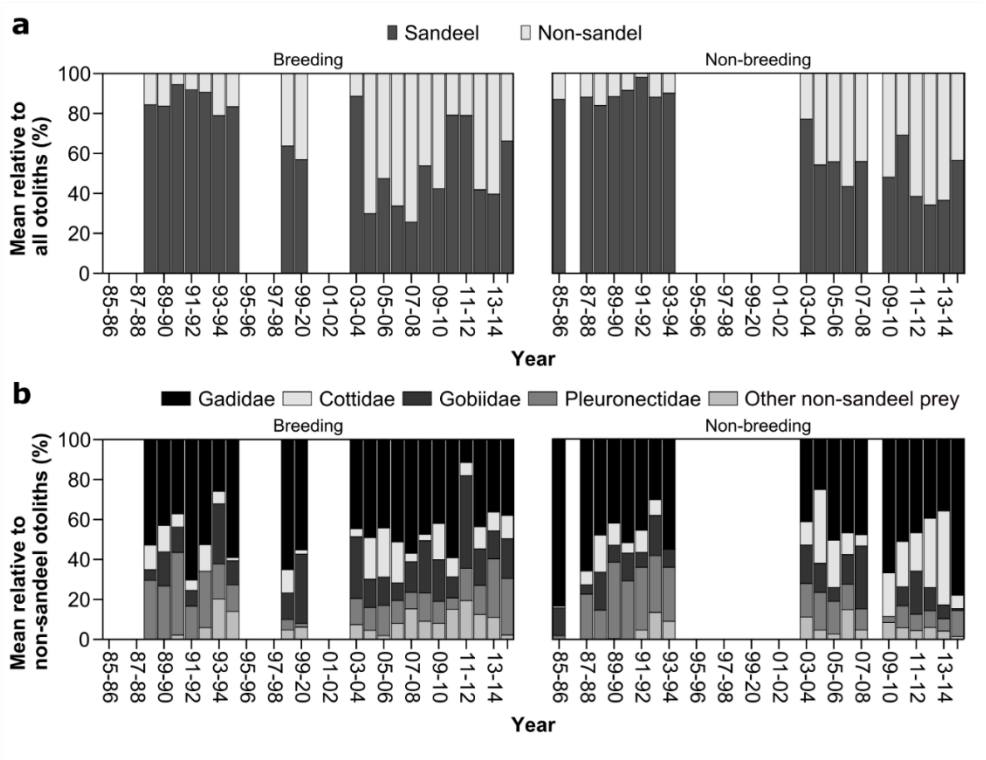

Figure 10 Interannual variation in breeding and non-breeding percentage numerical abundance, expressed as the mean across pellets between 1985-86 and 2014-15, for: a) sandeels (relative to all prey), and b) non-sandeels (relative to all non-sandeel prey). Blank years are those in which no pellets were collected. Values presented as percentages to aid comparison with frequency of occurrence.

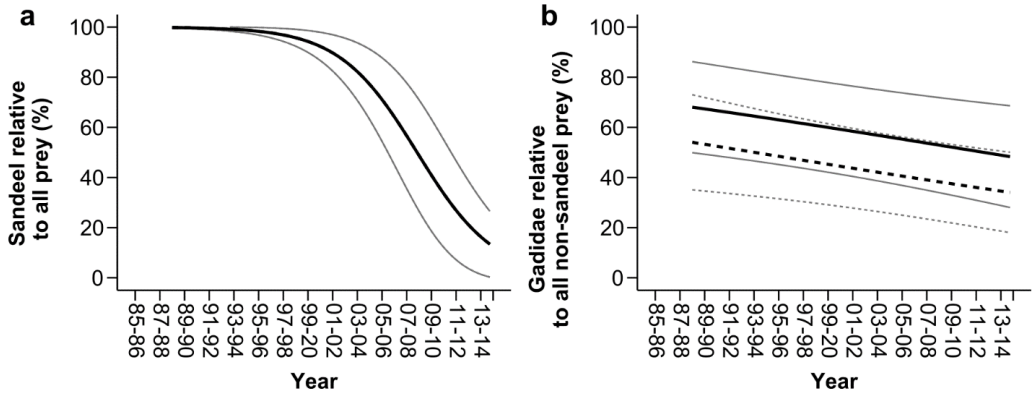

Figure 11 Fitted lines and 95% confidence intervals for percentage numerical abundance for: a). sandeels (relative to all prey), and b). Gadidae (relative to all non-sandeel prey) between 1988-89 and 2014-15. Plots with a single line indicate year effect only. Plots with two fitted lines indicate differences between periods (breeding period: solid line; non-breeding period: dashed line). Values presented as percentages to aid comparison with frequency of occurrence.

Table 11 Model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on sample-level Prey Richness, and linear

and quadratic trends in annual Prey Richness. Annual Prey Richness is fitted with a log(number of pellets year^{-1}) offset. Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z values, number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ω_i). Due to the large number of prey types and models, I only report those models within 10 AICc points of the top model, which is shown in **bold** (for full model selection tables see Appendix 2.5 Table A9). Models with similar levels of support as the top model indicated with †.

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
Sample-level Prey Richness	**1**	***Year + Period + Year*Period***				**5**	**0.00**	**1.00**
		Year	**0.37**	**0.04**	**8.95**			
		Period (NB)	**0.14**	**0.06**	**2.31**			
		Year*Period (NB)	**-0.20**	**0.04**	**-5.23**			
Annual Prey Richness	**1**	***Year + Year^2***				**5**	**0.00**	**0.66**
		Year	**0.93**	**0.26**	**3.62**			
		Year^2	**-0.86**	**0.37**	**-2.31**			
Annual Prey Richness	2†	*Year*				4	1.33	0.34
		Year	1.23	0.27	4.63			

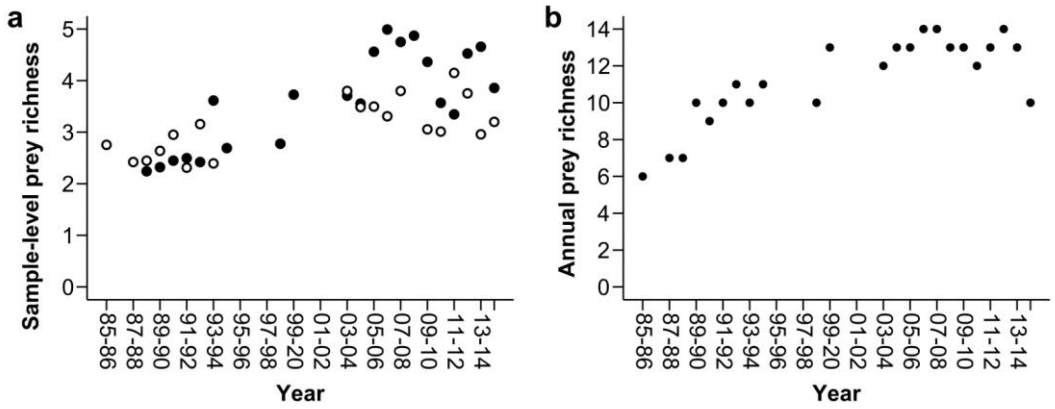

Figure 12 Interannual variation in a) mean sample-level Prey Richness per year during the breeding period (●) and non-breeding period (○); and b) annual Prey Richness between 1985-86 and 2014-15.

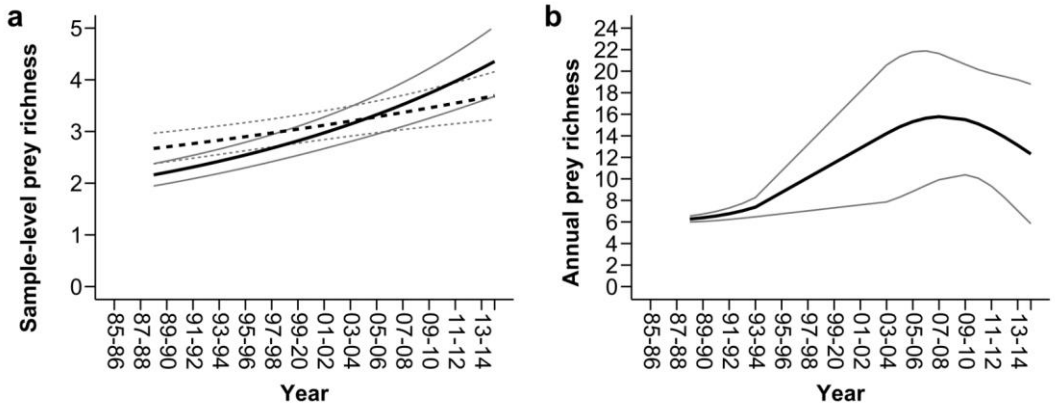

Figure 13 Fitted lines and 95% confidence intervals for modelled a) sample-level Prey Richness and b) annual Prey Richness between 1988-89 and 2014-15. Plots with two fitted lines indicate differences in trends between periods (breeding period: solid line; non-breeding period: dashed line). The linear and quadratic terms in the sample and annual Prey Richness plots appear as quadratic and cubic terms, respectively, due to the Poisson distribution of the data.

DISCUSSION

I identified dramatic changes in the diet composition of full-grown European shags *Phalacrocorax aristotelis* (hereafter shag) on the Isle of May over the past three decades both during and outside the breeding season. The dominance of lesser sandeels *Ammodytes marinus* (hereafter sandeel) decreased, with the decline in sandeel occurrence more marked during the non-breeding period. In contrast, the frequency of Gadidae, Cottidae, Pleuronectidae and Gobiidae increased. Prey richness also increased over the course of the study, in particular during the breeding period. These marked changes highlight the importance of monitoring changes in diet composition throughout the annual cycle.

DIETARY CHANGE

My findings of an overall decline in the dietary contribution of sandeel throughout the annual cycle, support my general prediction that changes in the importance of sandeels over time would be similar in breeding and non-breeding diets, since local sandeel populations are resident (Boulcott *et al.* 2007). One explanation for this year-round reduction is climate-mediated alterations in the abundance, availability or profitability of sandeels associated with rising temperatures in the North Sea (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009). Similar dietary changes have been observed in other seabird populations in response to changes in prey availability (Miller and Sydeman, 2004; Gaston and Elliott, 2014; Green *et al.*, 2015). In chapter 2 I also recorded a reduction in the length of sandeels fed to nestling shags at this colony over the past three decades, which, due to the negative, non-linear relationship between calorific content and sandeel size (Hislop, Harris and Smith, 1991; Wanless *et al.*, 2005), may be linked to the decreasing prevalence in shag diet. However, due to substantial digestive erosion of sandeel otoliths in pellets (Johnstone *et al.*, 1990), it was not possible to use otolith length-fish length relationships to infer changes in sandeel length in this study. With flexible foraging behaviours, as evidenced by the wide range of prey types exploited throughout their range, shags may be able to adjust their diet in response to availability and quality of alternative prey. Such flexibility may be a key mechanism underpinning the dietary

trends observed in this study, such that sandeel may have become scarcer or lessened in profitability compared to alternative prey, which may themselves have become more abundant or profitable. Data suggest that the energy density of alternative prey is similar to sandeels (Spitz *et al.*, 2010). However, in the absence of estimates of prey availability or capture rates, it is not possible to fully establish the causes underpinning these temporal patterns in diet composition. Industrial fisheries may also reduce the availability of sandeels, with knock-on effects on seabird diet composition. However, the sandeel fishery off eastern Scotland did not overlap spatially with the foraging distribution of this shag population (Figure 14; Bogdanova *et al.* 2014). Furthermore, the fishery was only operational between 1990 and 1999 (Daunt *et al.*, 2008). As such, I would have expected a stepped reduction in sandeel occurrence in the diet over this period, which was not what I found. Similarly, Wanless *et al.* (2018) did not record a reduction in sandeel occurrence in the diet of the seabird community breeding at the colony during the 1990s. I therefore consider it unlikely that top-down fishing pressure was driving the observed trends in sandeel dietary contribution.

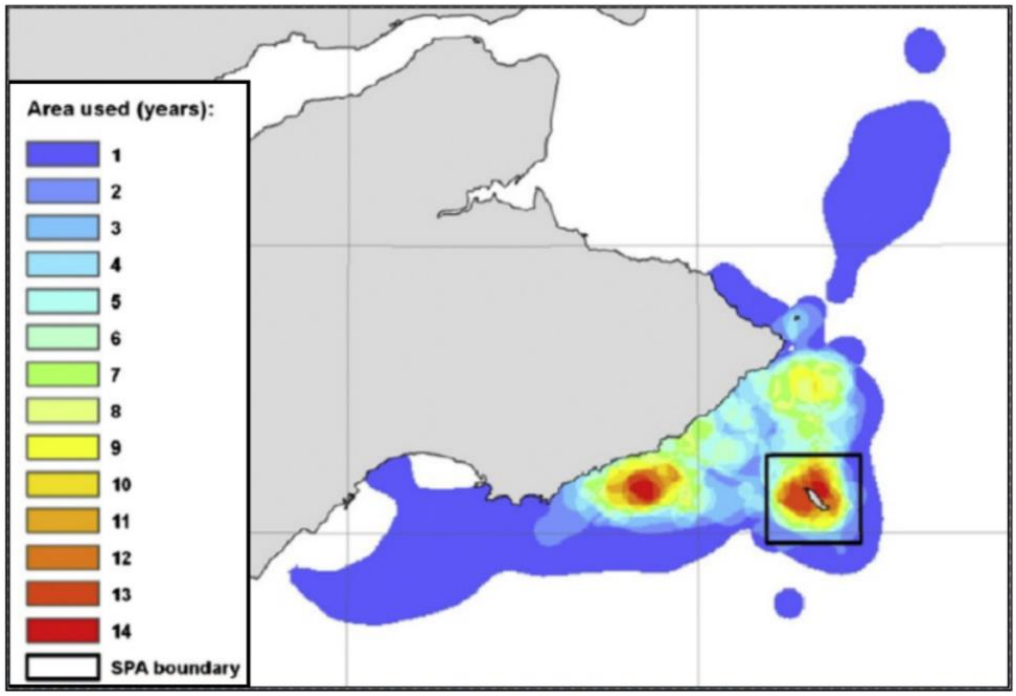

Figure 14 Consistency in shag foraging areas within areas of active use (95%), between 1987 and 2010 (figure provided by Maria Bogdanova). Shags predominantly feed around the colony or in two distant locations centred to the West and the North of the Isle of May (Bogdanova et al., 2014).

The steeper decline in sandeel frequency of occurrence during the non-breeding period may be linked to reduced foraging capacity at this time of the year, as a result of shortened day length, adverse weather and absence of sandeels in the water column, apart from a brief period during spawning (Wright and Bailey, 1993; Frederiksen *et al.*, 2008; Daunt *et al.*, 2014). Accordingly, any changes in overall prey availability over the course of the study might have had a more pronounced effect on diet composition at this time of year than during the breeding season. However, no seasonal difference in the rate of change was apparent in sandeel numerical abundance. This disparity with sandeel occurrence may arise because numerical abundance is quantified as the proportion relative to other prey, which themselves may have shown seasonal differences in trends. However, I could not test this since I could not distinguish changes in sandeels from reciprocal changes in other prey. Whatever the mechanism, the lack of difference between breeding and non-breeding periods in the trend in numerical abundance of sandeels relative to other prey suggests that this species has shown similar declines throughout the year in terms of biomass consumed. The overall reduction in frequency of sand is in line with these conclusions. Sand ingestion likely reflects accidental ingestion when foraging for sandeels, since shags generally extract sandeels directly from within the sand sediment (Watanuki *et al.* 2008), whereas other prey species that live in these habitats, such as Pleuronectidae and Callionymidae, are more likely captured on the sea floor.

The increase in dietary frequency of Gadidae accords with recent evidence of a distributional shift into Scottish waters of some Gadiformes in recent years (Cormon *et al.*, 2014), including saithe *Pollachius virens*, the principle prey of shags in some populations. Pleuronectidae frequency also increased in the diet over the last thirty years, so shags may have continued to forage in sandy areas through the course of the study, but increasingly targeted Pleuronectidae, and other prey associated with sandeel habitats, such as Callionymidae, rather than sandeels. Gobiidae also increased, but this prey class is predominantly associated with rocky areas, which accords with past work on this population demonstrating the use of multiple habitats (Watanuki *et al.* 2008). Gadidae otoliths relative to other non-

sandeel prey reduced over the study, suggesting that other non-sandeel prey have increased more rapidly than Gadidae. However, there was strong evidence that Gadidae numerical abundance relative to other non-sandeel prey was consistently higher during breeding. This is in contrast to Lilliendahl and Solmundsson (2006) who observed a higher prevalence of Gadidae in Icelandic shag pellets during winter. One possible explanation is that many Gadidae species use inshore waters as nursery grounds, with immatures moving into shallow, coastal feeding areas in the Firth of Forth during summer (Bergstad, Jørgensen and Dragesund, 1987; Heessen, Daan and Ellis, 2015).

One consequence of these dietary changes is that both sample-level and annual Prey Richness increased over the study, with the latter peaking in 2007. Long-term dietary diversification has also been observed in other seabird species in response to changes in prey availability (Gaston and Elliott, 2014). The parallel increase in diversity at the single pellet and whole year scale suggests that, on average, the population is now exhibiting an individual generalist/population generalist structure of resource use (Bolnick *et al.*, 2003). Seasonal patterns of sample-level Prey Richness changed over the study, such that the increase was more pronounced during breeding, in line with seasonal differences in the pattern of change among Pleuronectidae and Gobiidae frequency of occurrence. Climate-mediated changes in fish populations have been widely reported in the North Sea, including changes in the abundance and distribution of many species (Perry *et al.*, 2005; Dulvy *et al.*, 2008). Thus, the dietary trends observed in my study population may be indicative of reductions in the abundance and availability of sandeel, increases in non-sandeel prey or a combination of both. These changes may vary among seasons, but without independent data on any abundance of these prey types it is currently not possible to distinguish these alternatives.

As predominantly benthic, inshore foragers, it is unlikely that substantial competition for prey resources occurs between shags and other seabirds in the Firth of Forth, which generally feed more pelagically and offshore of the Isle of May. This is particularly true in the winter months, when the vast majority of seabirds are away from the Isle of May. However, considerable competition for sandeel and other prey

may occur throughout the year with other marine top predators, including pinnipeds, cetaceans and large predatory fish. Such competition may be particularly important during winter when a colony of ~2400 grey seals *Halichoerus grypus*, which prey heavily on sandeel, raise their young on the Isle of May (SNH, 2016). Prior to and during pupping large numbers of adult, female seals may compete with shags throughout their foraging habitats, while post-weaning, large numbers of juvenile seals may be highly dependent on the sandeel populations in close proximity to the island, leading to substantial competition with overwintering shags. Such effects may be particularly important given the concurrent decrease in sandeel availability and increase in seal breeding numbers recorded throughout the UK over the past three decades (Hanson and Hall, 2015). Gadidae populations have also increased in some Scottish waters in recent years (Cormon *et al.*, 2014), with immature individuals using inshore areas used by shags as juvenile nursery grounds (Bergstad, Jørgensen and Dragesund, 1987; Heessen, Daan and Ellis, 2015). Thus, although shags feed on young age classes of Gadidae, larger and older Gadidae may exert considerable top-down predation pressure on sandeel stocks (Engelhard et al., 2014). Therefore there are numerous biotic factors which may have contributed to the dietary trends observed in this study, but due to a lack of data could not be included in this analysis.

LIMITATIONS

It is important to recognise the limitations of estimating year-round diet from pellets when interpreting my results. The most important limitation of pellet analysis is the potential for underrepresentation of soft-bodied or easily digestible prey (Barrett *et al.*, 2007). For example, Pholidae and Callionymidae (the otoliths of which are poorly sampled by pellet analysis) can form a substantial proportion of chick diet in this population (chapter 2 but were recorded infrequently in pellets. One important consequence of this is patterns of long-term change over time might have been different had I been able to detect all prey types. In particular, the increase in diversity over the course of the study may be greater than I could demonstrate if more digestible prey than sandeels have become more common in the diet throughout the year, as indicated from my diet data obtained from regurgitates (chapter 2). A further limitation of my study is that I had to pool all sandeel age-

classes. As a result, I could not examine temporal and seasonal patterns in the relative contribution of different age classes, in contrast to my analysis of diet from regurgitations (chapter 2). Another consideration is that due to substantial differences in detection rates with sandeel size (i.e. larger fish are better represented in pellets; Johnstone *et al.* 1990), some of the observed reduction in sandeel relative numerical abundance may have been exacerbated by changes in detectability, since average sandeel length declined over the course of the study (chapter 2). However, given the dramatic trends observed in this study and the comparatively small decrease in sandeel size observed in chick diet (from in 104.5 mm 1988 to 92.0 in 2014), I consider my observation of a decline in sandeel abundance to be robust to this limitation. Finally, uncertainty in the date of pellet production could also have affected my results, for example by assigning pellets to the wrong period. However, given the length of non-breeding and breeding periods (several months) compared with the maximum likely duration between pellet production and collection (ca. two weeks), and the fitting of month as a random term in my models, I do not consider that this error would have had a strong impact on my results.

Demographic and conservation implications

The year-round reduction in the importance of sandeels in shag diet and associated dietary diversification may have important demographic consequences. In shags, the majority of mortality occurs in winter (Aebischer, 1986; Harris and Wanless, 1996; Frederiksen *et al.*, 2008), linked to foraging capacity in more challenging environmental conditions (Daunt *et al.*, 2006, 2014; Lewis *et al.*, 2015). Such changes may also be important during pre-breeding, when diet composition can be a key determinant of subsequent reproductive success (Sorensen *et al.*, 2009). Prey availability during the breeding season is also a key determinant of breeding success (Daunt *et al.*, 2001; Frederiksen, Mavor and Wanless, 2007). Crucially, effects on fitness are likely to depend on the relative profitability of different prey types throughout the annual cycle (Hislop, Harris and Smith, 1991; Litzow *et al.*, 2004). Due to the difference in habitat associations between prey types, the dietary change observed may also have important implications for shag foraging distributions (Bogdanova *et al.*, 2014; Michelot *et al.*, 2017). The increase in proportion of non-

sandeels in the diet could alter interactions with anthropogenic activities, such as offshore renewable developments or recreation. Shags in this population are partial migrants, whereby a proportion of individuals remain resident throughout the year while the remainder migrate (Grist *et al.* 2014). Studies that estimate diet composition during the non-breeding period throughout the population range would deliver a more complete picture of the potential implications for population dynamics and conservation management.

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Chapter 4: Productivity increases and phenology advances in a marine top predator over five decades

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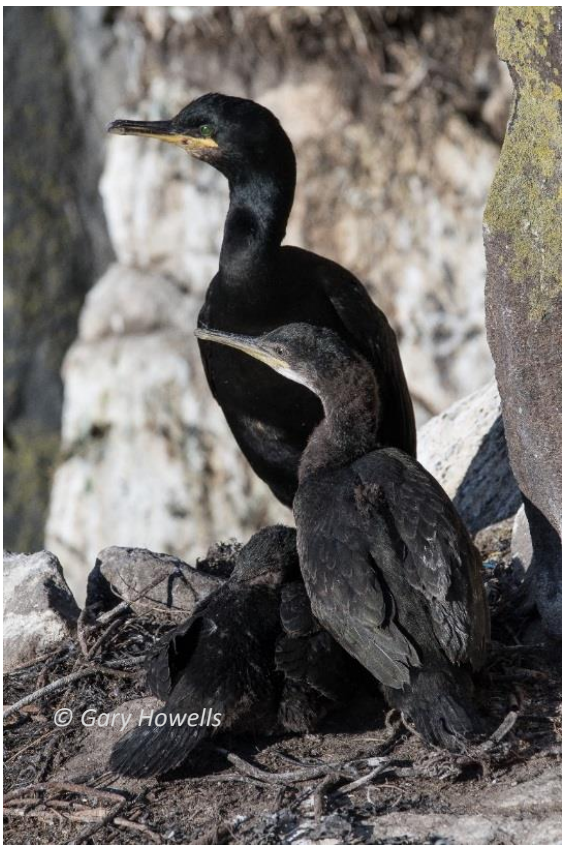

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ABSTRACT

Climate change is driving long-term trends in marine, freshwater and terrestrial ecosystems across the globe. Marine environments are displaying some of the most rapid rates of change in response to ocean warming. At the apex of these systems, marine top predators have shown pronounced population declines due to direct climatic impacts and indirect effects, whereby climate drives changes at lower trophic levels. These impacts may have arisen from immediate impacts on demographic rates, or delayed effects, whereby events in one period have downstream consequences in subsequent periods. These processes may have affected populations concurrently, so it is critical that studies analyse these effects simultaneously using long-term data sets of environmental and demographic change. In this study, I quantified the long-term trends and drivers of productivity in a population of European shags *Phalacrocorax aristotelis* between 1965 and 2016. Using a dataset comprising 15,359 breeding attempts, I found that mean productivity actually increased by 16% over the course of the study. This trend was strongly related to breeding phenology, which has advanced by an average of 26 days over the 51 year period. Late winter wind conditions determined interannual variability around the productivity trend. I also examined the factors underpinning the trend in breeding phenology, and found that birds bred earlier following warmer late winter Sea Surface Temperatures (SST) and a higher breeding productivity in the previous year. SST in the previous year explained the variability around the trend, such that timing of breeding was later following warmer SST in the previous year. Overall, my analysis demonstrated that SST and past reproductive performance, mediated via advancing phenology, were linked to the positive trend in breeding productivity observed within this population. These results demonstrate a rare example among long-lived top predators of a positive climate-mediated demographic consequence, which may have important implications for population demography and resilience to predicted future environmental change.

INTRODUCTION

Climate change is driving long-term trends in environmental conditions, trophic structure and species abundance in terrestrial, freshwater and marine ecosystems across the globe (Walther *et al.*, 2002; Parmesan, 2006; Walther, 2010; IPCC, 2014). These environmental trends are playing an important role in the population dynamics of higher trophic levels, by altering key demographic parameters such as breeding productivity and survival (Stenseth *et al.*, 2002). Climate-mediated impacts are fundamentally altering the structure and functioning of marine ecosystems (Hoegh-Guldberg and Bruno, 2010; Poloczanska *et al.*, 2013), which despite slower warming in the oceans compared to land (IPCC, 2014), are displaying faster rates of change than many terrestrial habitats (Edwards and Richardson, 2004; Burrows *et al.*, 2011). At the apex of these systems, many marine top-predator populations are displaying marked trends in key demographic rates in response to these environmental changes (Hoegh-Guldberg and Bruno, 2010; Doney *et al.*, 2012; Sydeman *et al.*, 2015). However, due to the complex nature of marine food webs and the quality of data required to test such effects, there remains limited understanding of the processes underpinning these demographic trends.

There are two principle processes whereby climatic change can affect the demography of marine top-predators (Thomas, 2010; Oro, 2014; Sydeman *et al.*, 2015). First, climatic effects can operate on organisms directly, whereby changes in short-term climatic variability, such as extreme weather events, cause direct mortality or affect individual condition, with impacts on survival rates (Boyce, Haridas and Lee, 2006; Moreno and Moller, 2011; Pipoly *et al.*, 2013; Descamps *et al.*, 2015). Second, indirect mechanisms can operate via bottom-up effects on the abundance or availability of lower trophic levels which propagate up the food web (Durant, Anker-Nilssen and Stenseth, 2003; Durant *et al.*, 2005; Parmesan, 2006; White, 2008). Direct climate-mediated mechanisms can affect the demography of top predators immediately, or have downstream consequences in later seasons (so called “carry-over effects”) or years (“lagged effects”). Indirect effects tend to affect top predator demography in later periods because bottom-up processes take time to propagate through food webs (Frederiksen *et al.*, 2006). Delayed effects may arise

through intrinsic processes, whereby demography is modulated by climate-driven intrinsic effort undertaken in previous years (Williams, 1966; Harrison *et al.*, 2011). Previous work has demonstrated that reproductive success in marine top predators is related to variation in climate (Aebischer & Coulson 1990; Croxall *et al.* 1990; Barbraud & Weimerskirch 2001). Environment-mediated costs associated with past reproduction may therefore modulate individual condition and performance in the current year (Inger *et al.* 2010, Catry *et al.* 2013, but see Bogdanova *et al.* 2017). Thus, in addition to the direct and indirect effects of climate on top predator productivity, environment-driven impacts on reproduction in one year may also have important downstream reproductive consequences in future breeding seasons.

In higher trophic levels breeding in seasonal environments, productivity is generally linked to the timing of breeding, such that earlier breeding is associated with greater reproductive output (Perrins, 1970; Clutton-Brock, 1988; Van Noordwijk, McCleery and Perrins, 1995). Thus, a key mechanism whereby direct and indirect climate-mediated mechanisms could affect top predator reproductive success is through alterations in the timing of breeding. Phenological trends have been observed in many marine ecosystems across the globe in response to changing environmental conditions, notably spring temperatures (Parmesan and Yohe, 2003; Edwards and Richardson, 2004; Thackeray *et al.*, 2016). Lower trophic organisms generally respond faster to ocean warming, which can lead to mismatches with prey availability during key life history events, such as reproduction (Cushing, 1990; Edwards and Richardson, 2004; Durant et al., 2005). Further, lagged effects between seasons may also modulate breeding phenology through effects on individual condition (Sorensen *et al.* 2009, Sheriff *et al.* 2015, Linton & Macdonald 2018, but see Bogdanova *et al.* 2011). Current conditions experienced on the breeding grounds may also be important in determining individual condition and thus the onset of breeding (Alvarez and Pajuelo, 2011; Ockendon, Leech and Pearce-Higgins, 2013). Thus, climate-mediated mechanisms may affect breeding productivity both directly or indirectly via changes in phenology (Miller-Rushing *et al.*, 2010). Further, as many marine top predator populations are displaying rapid declines (Pauly *et al.*, 1998; Heithaus *et al.*, 2008; Paleczny *et al.*, 2015), reproduction may also be modulated by

density-dependent effects, which may operate directly on breeding productivity (Stokes and Boersma, 2000; Forster and Phillips, 2009) or mediated via effects on phenology (Votier *et al.*, 2009; Cordes and Thompson, 2013). Negative density dependent effects may occur via competition for resources, such as breeding locations or food (Skogland, 1985; Elgar, 1989; Lewis, Sherratt, *et al.*, 2001), while positive effects of density include reduced predation pressure or social information transfer (Stephens and Sutherland, 1999; Danchin, 2004). In summary, both current and past climate conditions may affect breeding productivity directly or indirectly, potentially mediated via changes in phenology and modulated by population density. Teasing apart this complex suite of processes is a significant challenge, requiring long-term data on top predator productivity and concurrent data on prevailing environmental conditions (Frederiksen and Haug, 2015). Thus, our understanding of the interplay between these processes and the drivers of marine top predator demography remains poorly understood (Santora *et al.*, 2016), yet is a priority in order to understand the responses of marine top predators to ongoing and predicted future environmental change.

Using a dataset collected over five decades, I tested the drivers of breeding productivity in a European shag *Phalacrocorax aristotelis* (hereafter shag) population breeding at a North Sea colony. Shags are strongly affected by weather conditions, with foraging capacity, survival and reproductive output lower during inclement weather (Daunt *et al.*, 2006, 2014; Frederiksen *et al.*, 2008; Newell *et al.*, 2015). Breeding phenology in this population is highly variable among years, suggesting it is sensitive to variation in environmental conditions (Frederiksen, Harris, *et al.*, 2004; Burthe *et al.*, 2012). Thus, interannual variation in breeding phenology may be a key factor underpinning breeding productivity at this colony. The population size at this colony is also highly variable, displaying a pronounced increase up until the mid-1980s followed by a marked decline (Frederiksen *et al.*, 2008). Finally, the North Sea has warmed substantially over the past three decades, increasing by 0.037°C yr^{-1} between 1982 and 2012 (Høyer and Karagali, 2016), with profound bottom up impacts on ecosystem structure and prey availability (Beaugrand, 2004; van Deurs *et al.*, 2009; ter Hofstede, Hiddink and Rijnsdorp, 2010). Associated with this warming,

the diet of shags in this population has diversified (chapters 2 and 3). Shag breeding productivity has been linked to lesser sandeel *Ammodytes marinus* availability around this colony (Frederiksen, Mavor and Wanless, 2007) and so the dietary trends observed may have important reproductive consequences. Thus, as a long-lived species that is strongly affected by both direct and indirect climatic conditions, displays substantial fluctuations in colony size and highly variable breeding phenology, the shag population on the Isle of May provides an excellent study system in which to test the following specific questions:

a) what is the trend in breeding productivity over the last five decades?
b) is any change in breeding productivity underpinned by a change in phenology?
c) what immediate and downstream factors including environmental conditions, past breeding productivity and population density dependence, are driving trends and variation in productivity?
d) are these effects acting directly on productivity or indirectly via impacts on phenology?

METHODS

DEMOGRAPHIC RESPONSE VARIABLES

The study was conducted on the Isle of May National Nature Reserve, southeast Scotland (56°11‘N, 02°33’W). Monitoring of breeding biology was conducted between 1965 and 2016. Breeding productivity was estimated annually between 1965 and 2016 (excluding 1972 for which no data was available). Chicks (n = 33,009; mean ± SD: 634 ± 369 year^{-1}; range: 39-1448) at accessible nests (n = 15,359; mean ± SD: 295 ± 157 year^{-1}; range: 21-640), were ringed with British Trust for Ornithology metal rings midway through the chick-rearing period and the number of chicks present at each nest was recorded. I used annual mean number of chicks per nest at ringing (hereafter brood size) as a measure of productivity. Although breeding success (number of chicks fledged per pair) is the most commonly used variable to quantify breeding productivity in seabird populations, in European shags *Phalacrocorax aristotelis* (hereafter shag), there is comparatively little mortality

between ringing and fledging at ca. 50 days in most years, with most chick mortality occurring in the first ten days after hatching (Daunt *et al.* 1999). Thus, brood size is likely to be a reliable proxy of breeding success. To test this, I compared brood size and breeding success over a shorter span of years (1986-2016) where both variables have been collected. Annually between 1986 and 2016, breeding success (number of chicks fledged; n = 3967; mean ± SD: 128 ± 73 year^{-1}; range: 14-317) was recorded from a sample of nests (n = 3,659; mean: 118 ± 64 year^{-1}; range: 42-288) in 9-14 monitoring plots distributed throughout the island (Newell *et al.*, 2015), using standardised methods (Walsh *et al.* 1995). Brood size and breeding success were highly correlated from 1986-2016 (R = 0.93; Appendix 3.1 Figure A1). This very high correlation demonstrated that brood size is a reliable measure of breeding success, allowing me to test trends and drivers over a longer span of years.

Breeding phenology was estimated as the annual median date on which ringing took place (hereafter ringing date). Although seabird breeding phenology is usually quantified using first/median egg laying dates, chick ringing generally takes place at a similar stage relative to the start of the season each year (chick age at ringing for 1997-2016, when estimates of chick age are available: n = 18,238; mean ± SD of annual means: 28 ± 2 days). Thus, ringing date likely provides a suitable proxy of breeding phenology in this population. To test this, I compared ringing date and laying date over the shorter span of years (1986-2016) where both sets of variables had been collected. Annually between 1986 and 2016, laying date was recorded at the same sample of nests as breeding success, using standardised methods (Walsh *et al.* 1995). From this, I calculated annual median laying date (hereafter laying date). Ringing date and laying date were also highly correlated from 1986-2016 (R = 0.97; Appendix 3.1 Figure A1; Frederiksen, Harris, *et al.* 2004, updated).

My principal analysis was undertaken on brood size and ringing date to ensure maximum temporal coverage (1965-2016). However, I repeated analyses on breeding success and laying date from 1986-2016 to ensure that my results were robust to the choice of productivity and phenology variable. Crucially, there was strong congruence between the two sets of analyses, and thus I report the brood size and ringing date analyses in the main text, with analysis of breeding success and

laying date provided in Appendix 3.2 (Table A10 to Table A17; Figure A2 to Figure A3).

Explanatory variables

To test the relative importance of direct and indirect environmental change on brood size, and whether these effects operate immediately, are delayed, or are mediated via ringing date, I selected the following suite of explanatory variables. Variables were collated between 1974 and 2016 (1973 for lagged variables) as this was the first year over which all explanatory variables was available. Thus, trends analyses of brood size and ringing date were undertaken between 1965 and 2016, and covariate analyses ran between 1974 and 2016. Additionally, I undertook a trends analysis of breeding success and laying date between 1986 and 2016.

Immediate effects

Proxies of sandeel availability

Availability of principal prey is a key determinant of demography in many seabirds (Monaghan *et al.*, 1989). Although the lagged, larval Sandeel Biomass Index has previously been shown as an important determinant of shag breeding productivity in this population (Frederiksen, Furness and Wanless, 2007), these data were unavailable for the majority of the study period. Thus, I utilised three proxies of lesser sandeel *Ammodytes marinus* (*hereafter* sandeel) availability in my analysis in order to determine whether changes in diet were linked to brood size: a) Sea Surface Temperature (hereafter SST); b) SST in the previous year; and c) diet.

Sandeel abundance is determined by SST via indirect bottom-up mechanisms (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009; Rindorf *et al.*, 2016). Monthly SST data were obtained from the German 'Bundesamt fur Seeschiffart und Hydrographie' (http://www.bsh.de) between 1973 and 2016, following Frederiksen *et al.* (2004). Spring SST (average of mean February and March; i.e. peak months of sandeel hatching; Macer, 1966; Wright and Bailey, 1996; Frederiksen *et al.*, 2011) were extracted for an inshore area surrounding the Isle of May (bounded by c. 56°0'N and 56°4'N, and 2°7'W and 2°3'W), encompassing the summer foraging range of this

population (Bogdanova *et al.*, 2014). 1+ sandeel form a substantial part of chick diet in this population, the proportion of which is determined by SST in the previous year. Thus, I also included SST lagged by one year. Although the variable was lagged, the mechanism through which I believe this effect to be operating is via impacts on sandeel availability in the current year and so I consider this effect to be a proxy of immediate prey conditions.

I also tested the effect of the proportion of sandeel in chick diet (hereafter proportion of sandeel), following methods in chapter 2. These data were available between 1985 and 2016, and so were only used in an additional analysis of brood size using a subset of years.

POPULATION SIZE

Changes in population size at this colony may impact brood size via density dependent effects, which have been shown to affect shag reproductive output (Potts, Coulson and Deans, 1980; Aebischer, 1985). Thus, to examine the effects of density dependence on brood size and ringing date I tested the effect of the number of breeding pairs, collected using standardised protocols (apparently occupied nests; see Walsh *et al.* 1995), hereafter referred to as population size.

PREVAILING WEATHER CONDITIONS

Shag foraging performance is strongly affected by wind in this population (Daunt *et al.*, 2006, 2014; Lewis *et al.*, 2015; Kogure *et al.*, 2016), which may alter the capacity of parents to provision the brood. Furthermore, young chicks are vulnerable to exposure to strong winds and heavy rain (Snow 1960, Aebischer 1985, Daunt *et al.* 1999, Velando *et al.* 1999). To test the effects of breeding season weather, hourly wind and rain data were obtained from Leuchars weather station (56°23'N, 2°52'W; c.28 km from the study site; http:// badc.nerc.ac.uk), between 1974-2016. Following Frederiksen *et al.* (2008), I calculated daily Onshore Component as mean daily wind speed (knots) * sin(mean daily wind direction), and set it to 0 if the wind direction was westerly i.e. between 180° and 360°. I used the first 28 days after median hatching date (hereafter early chick-rearing period) to encompass the period of chick vulnerability, and to match the duration of the February Onshore Component variable used in Frederiksen *et al.* (2008). To create this variable, I selected the 28

day period (the mean chick age at ringing) prior to and including the ringing date, and calculated summed breeding season Onshore Component (hereafter breeding Onshore Component) and Total Precipitation (hereafter breeding Total Precipitation) during the early chick-rearing period.

DELAYED EFFECTS

PREVIOUS BROOD SIZE AND RINGING DATE

Long-lived species, such as shags, must balance the trade-off between current reproductive investment and lifetime fecundity (Williams, 1966). Costs associated with previous reproduction may alter individual condition and, in turn, breeding phenology and breeding productivity in the current year (Inger *et al.*, 2010; Catry *et al.*, 2013). Breeding productivity likely represents an integrated measure of environmental conditions (Frederiksen, Mavor and Wanless, 2007), so any relationship between past and current reproductive output may equate to a lagged effect of environmental conditions in the previous year. Therefore, I included ringing date and brood size in the previous year in the analysis to test for any downstream effects of costs associated with previous reproduction.

FEBRUARY WEATHER

Winter weather conditions, in particular onshore (i.e. easterly) winds and precipitation during February, affect breeding phenology in this population (Aebischer, 1986; Aebischer and Wanless, 1992; Daunt *et al.*, 2006, 2014). Survival probability is also lower when winter weather is poor (Frederiksen *et al.*, 2008), and surviving birds could experience reduced individual condition with knock-on effects on productivity. Thus, daily Onshore Component values were summed over February in each year to calculate an annual February Onshore Component in line with Frederiksen *et al.* 2008. February Total Precipitation comprised summed hourly precipitation over February in each year. Both variables had the same duration and method of processing the data as the breeding weather variables.

STATISTICAL MODELLING

RATIONALE

Given the prediction that breeding phenology influences breeding productivity in shags, elucidating the drivers of brood size also requires an understanding of which factors determine ringing date. Thus, I structured my analysis in two steps. First, I tested the explanatory covariates, including ringing date, of trends and variability in brood size. Then, in a second step, I tested the explanatory covariates of trends and variability in ringing date, including only those variables that preceded ringing date in the year of interest. This structured analysis allowed me to determine whether the explanatory covariates operate directly on brood size or mediated via impacts on ringing date. All data manipulation and statistical modelling was conducted using the R programming language (R Development Core Team, 2016).

TRENDS ANALYSES

As the focus of my analysis was to test the effects of trends in environmental covariates and causes of underlying variation on my shag demographic parameters, it was first necessary to test for trends in each of my explanatory covariates. Initial plotting suggested potential serial autocorrelation in the productivity and phenology response variables. Thus, to test for trends in productivity I fitted Generalised Linear Mixed Models (hereafter GLMMs) using the Penalized Quasi-likelihood methods in the *glmmPQL* function, which automatically accounts for over dispersion (*MASS* package, Venables & Ripley 2002). To avoid predicted values being higher than the maximum number of chicks fledged in this population (4; Harris *et al.* 1994) or below 0, I adopted a binomial modelling approach for brood size (Cook *et al.*, 2014; Carroll *et al.*, 2015). Thus, brood size was modelled as the total number of chicks present within all nests at ringing / (number of nests where ringing was undertaken * 4). For ringing date I fitted Linear Mixed effects models (hereafter LMMs) in the *lme* function (*MASS* package, Venables & Ripley 2002). I chose these methods for the trends analyses as they can include an autoregressive term (AR) to account for serial autocorrelation between data points, which is not available in other packages. However, information-theoretic approaches, such as the *Akaike Information Criterion*, are not available using *glmmPQL*. Thus, model selection was conducted via

backwards stepwise deletion, which remains a valuable tool where other methods are not possible (Murtaugh, 2014). Binomial GLMMs with a log-link function were fitted for productivity variables and Gaussian LMMs for phenology variables. To fit within the GLMM/LMM framework, I also included a dummy random effect of 1 for each data point. Visual inspection of the data suggested that trends may have been non-linear, so I fitted a global model containing a linear and quadratic effect of year.

Several environmental parameters are displaying pronounced trends in the North Sea (Burthe *et al.*, 2012). Thus, trends in environmental conditions may be key factors underpinning any trends in shag demography. To investigate whether this was the case, I first needed to test whether trends existed in the explanatory covariates. Consequently, I tested for linear and quadratic trends in each of the predictor variables (SST, breeding Onshore Component, breeding Total Precipitation, population size, February OC, February Total Precipitation) using the *lme* function, including an AR term, in the MASS package. To achieve normality and conform to model assumptions I $\log_{10}$ transformed breeding population size. For the proportion of sandeel, I fitted a binomial GLMM with a logit-link function and AR term using *glmmpql*.

COVARIATE MODELS

To test the determinants of brood size I fitted GLMMs with a binomial error and logit-link function using *glmer* function, in the *lme4* package (Bates *et al.* 2015). To account for overdispersion, year was included as an annual-level categorical random effect. I fitted a global GLMM containing each of my explanatory variables: SST, SST t-1, population size, breeding Onshore Component, breeding Total Precipitation, ringing date, ringing date t-1, brood size t-1, February Onshore Component, and February Total Precipitation. As the diet data were only available over a shorter run of years, a supplementary analysis was conducted to identify whether diet was a better predictor of brood size than those variables identified in the full model selection process.

To test the determinants of ringing date I fitted a global Linear Model (hereafter LM) including the following variables: SST, SST t-1, breeding population size, ringing date t-1, brood size t-1, February Onshore Component, February Total Precipitation. It was

not necessary to include an AR term in models of brood size and ringing date, as brood size t-1 and ringing date t-1, were included as fixed effects in the model selection process.

Model comparison was conducted using Akaike's Information Criterion corrected for small sample sizes (AICc). Models within 2 AICc points of the best supported model (lowest AICc) were considered to have strong support, unless they contained an additional parameter, in which case they were regarded as uninformative and not considered (Burnham and Anderson, 2002; Arnold, 2010). For all models, the distribution of residuals indicated no violation of normality or homoscedasticity assumptions (Zuur *et al.*, 2009).

As sufficient temporal coverage of predictor variables did not commence until 1974, covariate models of brood size and ringing date were restricted to 1974-2016 (42 years). The supplementary dietary analysis of brood size was conducted between 1985-2016. I had no biological *a priori* reason to test for interaction terms and thus my analysis considered main effects only. All explanatory variables were scaled and centred to make effect sizes comparable (mean = 0) and to avoid model convergence issues. Due to the large number of models for each response, I present those with AICc < 2 in the main text, with additional models presented in Appendix 3.3 (Table A18) and Appendix 3.4 (Table A19).

A requirement of the GLMM/LM modelling approach is that covariates within the same models are not collinear. Thus, to test for collinearity between covariates, I calculated Pearson's Correlation Coefficients between each of my predictor variables (Appendix 3.5 Table A20). Where substantial collinearity was identified ($r > 0.6$), those variables were not permitted together in the same candidate model. This included SST and February OC ($r = -0.67$) and brood size t-1 and ringing date t-1 ($r = -0.68$).

When trends are present in both response and explanatory variables spurious results may occur (Grosbois *et al.*, 2008). Thus, as I identified temporal trends in some of the covariates, I undertook a supplementary detrending analysis, in which a linear, fixed effect of year was fitted in all explanatory models of brood size and ringing date

during the modelling process. In doing so, I removed any temporal trends from the response variables. Model support was compared between the non-detrended and detrended models. Where differences occurred this suggests that support identified in the non-detrended analysis may be due to correlation with a third variable that is also displaying a temporal trend, and should be treated with caution. I present the non-detrended models in the main text with detrended models provided in Appendix 3.6 (Table A21) and Appendix 3.7 (Table A22).

Where there was an association between a response and a covariate, that itself was showing the same directional trend, I interpreted it as a potential driver of the trend. In contrast, where there was an association with a covariate that was not showing a directional trend, or was showing a trend in the opposite direction, I interpreted it as a potential driver of annual variability around the trend.

As a Poisson error structure could be a valid distribution for brood size, I undertook a further supplementary analysis, in which I fitted GLMMs with a Poisson error distribution and a log(number of nests) offset. Results were comparable between the two modelling approaches and thus I consider the use of binomial analyses appropriate. Binomial models are presented in the main text with Poisson models presented in Appendix 3.8 (Table A23).

RESULTS

TRENDS IN BREEDING PRODUCTIVITY AND PHENOLOGY

I identified striking trends in breeding productivity and phenology, such that European shags *Phalacrocorax aristotelis* (hereafter shag) in this population now raise more chicks and breed earlier than half a century ago. Brood size increased over the study, by 16%, from 1.99 chicks nest^{-1} in 1965 to 2.30 chicks nest^{-1} in 2016, equivalent to < 0.01 chicks year^{-1} (Figure 15a, Table 12). However, breeding success more than doubled between 1986 and 2016, from 0.77 chicks fledged nest^{-1} to 1.72 chicks fledged nest^{-1}, an increase of 126% over 30 years, equivalent to 0.03 chicks year^{-1} (Figure 15b; Table 12).

Ringing date advanced over the study, by a total of 26 days, from the 198th day of the year^{-1} (~16th July) in 1965 to 172nd (~20th June) in 2016, equivalent to 0.62 days year^{-1} (Figure 15c**;** Table 12). Lay date advanced even more rapidly between 1986 and 2016, by 35 days in total, from the 142nd day of the year (~22 May) to the 107th day of the year (~16th April); equating to 1.13 days year^{-1} (Figure 15c; Table 12).

There was evidence of positive autocorrelation in both brood size (Phi = 0.72) and breeding success (Phi = 0.40; Table 12), indicating that productivity was similar between successive years. Similarly, there was also evidence of serial autocorrelation in ringing date (Phi = 0.39) and laying date (Phi = 0.34), again indicating that phenology was similar between successive years (Table 12).

Table 12 Trends analysis of brood size (chicks nest^{-1}) and ringing date (day of year) between 1965 and 2016, and breeding success (chicks nest^{-1}; Breed. succ.) and laying date (day of year) between 1986 and 2016. Mean ± SD, maximum and minimum observed values reported for each response variable. Estimates (±SE), t- and p-values are reported for each model identified via backwards-stepwise deletion, along with a measure of autocorrelation, Phi.

Response	Mean ± SD	Min	Max	Trend	Est	SE	t	p	Phi
Brood size	2.08 ± 0.24	1.52	2.54	Linear	0.09	0.04	2.13	0.038	0.72
Breed. succ.	1.15 ± 0.56	0.18	2.10	Linear	0.59	0.18	3.3	0.003	0.40
Ringing date	185 ± 17	157	231	Linear	-6.93	2.73	-2.54	0.140	0.39
Laying date	125 ± 18	97	181	Linear	-17.69	6.07	-2.92	0.007	0.34

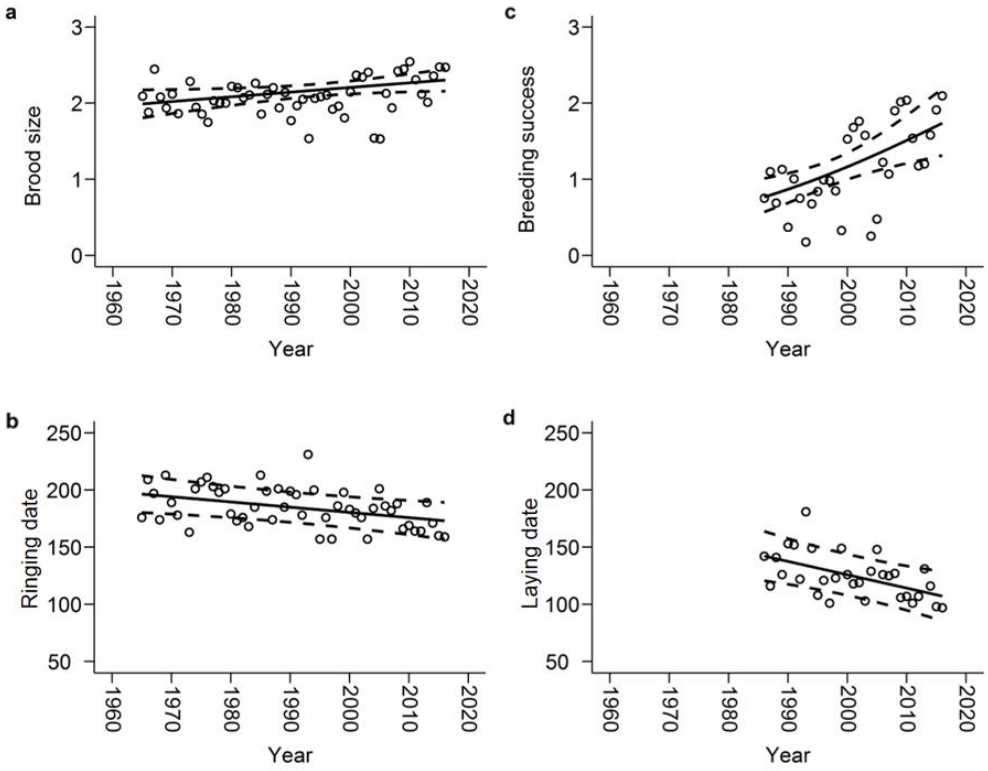

Figure 15 Temporal trends in a) brood size (chicks nest-1); and b) ringing date (day of year) between 1965 and 2016; and c) breeding success (chicks nest-1) and d) laying date (linear trend) between 1986 and 2016. Solid line indicates linear tend and dashed lines indicate confidence intervals.

TRENDS IN EXPLANATORY COVARIATES

SST increased linearly over the study from 5.23°C in 1974 to 6.13°C in 2016, and there was moderate evidence of autocorrelation between years (Phi = 0.4; Table 13). There was a substantial decline in the proportion of lesser sandeel *Ammodytes marinus* (*hereafter* sandeel) in the diet, from 0.96 in 1985 to 0.48 in 2016, and there was strong evidence of serial autocorrelation between years (Phi = 0.79; Table 13). February Onshore Component reduced markedly over the study from 98.03 Onshore Component (OC) in 1974 to 18.04 OC in 2018, but there was limited evidence of autocorrelation between years (Phi = 0.05; Table 13). There was no evidence that any of the trends identified were quadratic (Table 13). No trends were identified in any of the other predictor variables (breeding Onshore Component and Total Precipitation, February Total Precipitation, and population size; Table 13).

Table 13 Trends analysis of each of my explanatory covariates between 1974-2016 (proportion of sandeel 1985-2016). OC = Onshore Component. TP = Total Precipitation. Mean ± SD, maximum and minimum observed values also reported for each response variable. Estimates (±SE), t- and p-values are reported for each model identified via backwards-stepwise deletion, along with a measure of autocorrelation, Phi. No trend was identified in February total precipitation, breeding Onshore Component, breeding total precipitation or breeding population size.

Response	Mean ± SD	Min	Max	Trend	Est	SE	t	p	Phi
February OC	58.06 ± 54.76	0.00	230.76	Linear	-23.91	7.89	-3.03	0.004	0.05
February TP (mm)	94.28 ± 63.51	7.40	283.30	-	-	-	-	-	-
Breeding OC	79.25 ± 42.27	0.47	182.39	-	-	-	-	-	-
Breeding TP (mm)	112.34 ± 54.45	8.80	243.90	-	-	-	-	-	-
SST (°C)	5.71 ± 0.57	4.15	6.78	Linear	0.25	0.10	2.64	0.012	0.40
Prop. of sandeel	0.79 ± 0.24	0.28	1.00	Linear	-0.98	0.35	-2.76	0.010	0.79
Population size	839 ± 467	259	1916	-	-	-	-	-	-

Explanatory covariates of brood size

The best supported model for brood size contained a negative effect of ringing date and a positive effect of February Onshore Component (Figure 16; Table 14; extended model selection table presented in Appendix 3.3 Table A18). Earlier years were associated with a larger brood size, from 2.39 chicks nest^{-1} at a ringing date of 157 days (~6th June) to 1.57 chicks nest^{-1} at 231 days (~19th August; Figure 16a). Higher February Onshore Component was associated with an increased brood size, from 2.01 chicks nest^{-1} at an OC value of 0 to 2.31 chicks nest^{-1} at an OC value of 231 (Figure 16b). The same variables were supported in the detrended analysis, with the best supported model containing an effect of ringing date, February Onshore Component, and year (Appendix 3.6 Table A21). In the analysis conducted with a Poisson error structure, the best supported model also contained an effect of laying date and February Onshore Component (Appendix 3.8 Table A23).

To test the effect of diet on brood size, I fitted an additional model containing an effect of ringing date, February Onshore Component, and the proportion of sandeel in the diet between 1985 and 2016 (Appendix 3.9 Table A24). The proportion

of sandeel in the diet had a positive effect on brood size, but only in the detrended analysis (Appendix 3.10 Table A25). There was little or no evidence that current or lagged SST, breeding season weather conditions, population size, February Total Precipitation, ringing date in the previous year and brood size in the previous year were important determinants of brood size.

Table 14 Model selection table and effect sizes for binomial GLMMs of brood size modelled between 1974 and 2016. OC = Onshore Component; TP = Total precipitation. t-1 = indicates that covariate is lagged by one year. For each fixed effect I report an estimate (± SE) and z-value. The number of parameters (k), difference in AICc relative to the best supported model (ΔAICc) and model weight (ω_i) relative to other models within 2 AICc are presented for each model. Only models with relatively strong support (ΔAICc <2) are presented. The best supported model is shown in bold.

Rank	Model	Est	SE	z	k	ΔAICc	ω_i
1	***February OC + Ringing date***				**4**	**0.00**	**0.09**
	February OC	**0.07**	**0.03**	**2.47**			
	Ringing date	**-0.20**	**0.03**	**-6.6**			
2	*Breeding TP + February OC + Ringing date*				5	0.85	0.06
	Breeding TP	-0.04	0.03	-1.32			
	February OC	0.07	0.03	2.23			
	Ringing date	-0.20	0.03	-6.76			
3	*February OC + Brood size t-1 + Ringing date*				5	1.70	0.04
	February OC	0.08	0.03	2.61			
	Brood size t-1	0.03	0.03	0.94			
	Ringing date	-0.18	0.03	-5.53			

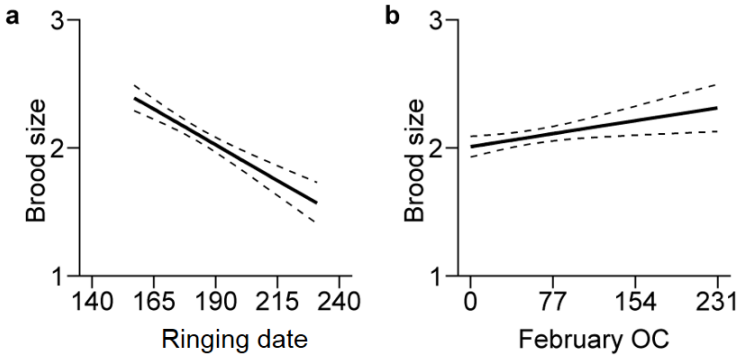

Figure 16 Fitted lines (±95 % CI) for the relationship between brood size and a) ringing date, and b) February Onshore Component. Values are displayed over the range for which data were included in the model. Predictions were made using binomial GLMMs, setting additional fixed effects at the mean value. Solid line indicates linear tend and dashed lines indicate confidence intervals.

Explanatory covariates of phenology

The best supported model for ringing date contained a negative effect of SST in the current year, a positive effect of SST in the previous year, and a negative effect of brood size in the previous year (Figure 17, Table 15, extended model selection table provided in Appendix 3.4 Table A19). Higher SST in the current year was associated with an earlier ringing date, from 202 days (~21st July) at 4.15 °C to 173 days (~22nd June) at 6.78 °C (Figure 17a). Conversely, higher temperatures in the previous year were associated with a later ringing date, from 172 days (~10th July) at 4.15 °C to 193 days (~20th June) at 6.78 °C (Figure 17b). Ringing date advanced from 203 days (~22th July) when brood size in the previous year was 1.50 chicks nest^{-1}, to 169 days (~18th June) when the brood size in the previous year was 2.54 chicks nest^{-1} (Figure 17c). Only one nested model, containing an effect of SST in the current year only and brood size in the previous year was within 2 AICc, indicating substantial support for these two variables. The effect of SST in the current year was removed from the best supported model in the detrending analysis of ringing date, with the best supported model containing an effect of SST and brood size in the previous year only (Appendix 3.7 Table A22). There was no evidence that population size, February weather or ringing date in the previous year were important determinants of ringing date.

Table 15 Model selection table and effect sizes for Linear Models of ringing date modelled between 1974-2016, respectively. TP = Total precipitation. t-1 = covariate lagged by one year. For each fixed effect within a model, I report an estimate (± SE) and t-value. For model comparisons the number of parameters (k), difference in AICc relative to the best supported model (ΔAICc) and model weight (ω_i) relative to other models within 2 AICc. Only models with relatively strong support (ΔAICc <2) are presented. The best supported model is shown in bold, and models with equal support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	Est	SE	t	k	ΔAICc	ω_i
1	***SST + SST t-1 + Brood size t-1***				**5**	**0.00**	**0.20**
	SST	**-6.27**	**2.34**	**-2.68**			
	SST t-1	**4.42**	**2.33**	**1.9**			
	Brood size t-1	**-8.12**	**2.22**	**-3.66**			
2	*SST + SST t-1 + Population size + Brood size t-1*				6	1.11	0.12
	SST	-5.9	2.34	-2.52			
	SST t-1	5.38	2.45	2.2			
	Population size	2.87	2.39	1.2			
	Brood size t-1	-8.23	2.21	-3.72			
3†	*SST + Brood size t-1*				4	1.24	0.11
	SST	-4.89	2.29	-2.13			
	Brood size t-1	-8.05	2.29	-3.52			
4	*SST + SST t-1 + February TP + Brood size t-1*				6	2.00	0.07
	SST	-6.04	2.36	-2.55			
	SST t-1	3.87	2.44	1.58			
	February TP	-1.86	2.33	-0.8			
	Brood size t-1	-8.28	2.24	-3.7			

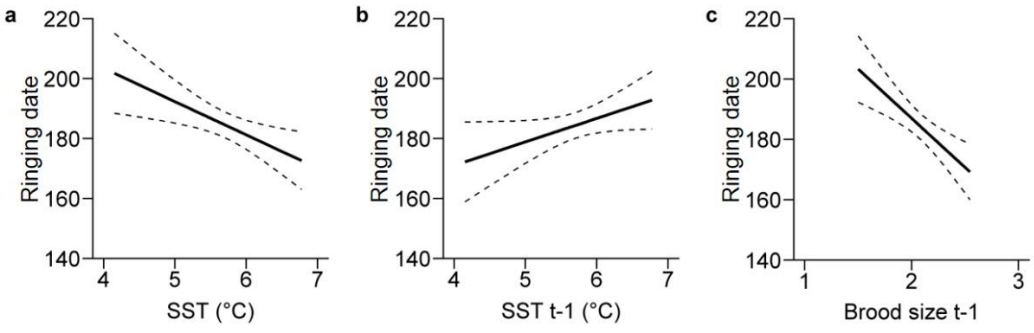

Figure 17 Fitted lines (±95 % CI) for the relationship between ringing date and a) SST in the current year, b) SST in the previous year and c) brood size in the previous year. Values are displayed over the range for which data were included in the model. Predictions were made using LMs, setting additional fixed effects at the mean value. Solid line indicates linear tend and dashed lines indicate confidence intervals.

DISCUSSION

Using a dataset spanning five decades, I identified a rare example among marine top predators of an increase in reproductive success over the last half a century in response to ongoing environmental change and lagged effects. Shags in this population now raise 16% more young per nest than at the start of the study. Over the same period, I observed a dramatic advancement in phenology, with breeding now approximately 26 days earlier than at the start of the study. Crucially, I demonstrate that the increase in productivity was related to earlier breeding, which in turn was linked to current SST and past productivity (Figure 18). February weather conditions and lagged SST affected the variability around the trends in productivity and phenology, respectively. These results indicate that the population may have the capacity to respond positively to climate-mediated alterations in the marine environment, which may confer some resilience to current and predicted future climatic change.

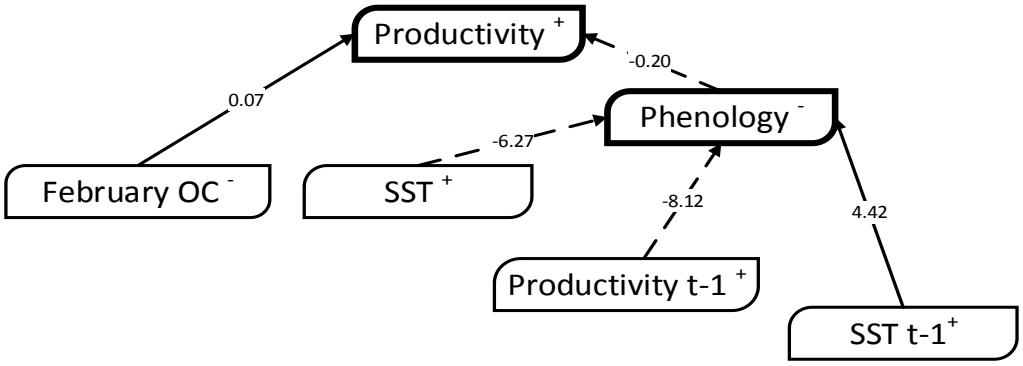

Figure 18 Schematic diagram of relationship between European shag *Phalacrocorax aristotelis* (hereafter shag) reproductive parameters (productivity: brood size; phenology: ringing date) and environmental covariates. t-1 indicates that covariates are lagged by a year. + indicates positive trend; - indicates negative trend. Solid lines indicate positive effects and dashed lines negative effects. Effect sizes for each covariate displayed on lines, but effect sizes are not comparable between the productivity and phenology variables due to the distribution of the response variables.

TRENDS IN DEMOGRAPHIC RESPONSE VARIABLES

Many marine top predators are displaying marked negative demographic trends in response to ongoing climate-mediated environmental change (Doney *et al.*, 2012;

Frederiksen and Haug, 2015; Sydeman *et al.*, 2015). This is particularly true in seabirds, the conservation status and population trends of which are declining rapidly (Croxall *et al.*, 2012; Paleczny *et al.*, 2015). Breeding failures have occured in many North Sea seabird populations over the last three decades (Cook *et al.*, 2014; McDonald *et al.*, 2015; Daunt, Mitchell and Frederiksen, 2017). However, in contrast to other studies in the region, I provide evidence of a substantial, linear increase in productivity over the past half a century. Globally there is no tendency for seabirds to advance or delay breeding phenology over time (-0.02 days yr^{-1}; Keogan *et al.* 2018). In contrast to this, I identified a dramatic advancement in shag breeding phenology on the Isle of May. However, Keogan *et al.* (2018) showed that some families, such as Suliformes (cormorants, gannets and boobies), are exhibiting pronounced variability in phenology, likely linked to local climatic/environmental conditions. In line with this, breeding phenology was highly variable by around a month over the study. Combined, the substantial increase in breeding productivity and rapid, but variable trend in breeding phenology, demonstrate that shags in this population are displaying flexible, but linked demographic responses to current environmental change.

Explanatory covariates of productivity

Breeding phenology is a key determinant of reproductive output in many avian species (Lack, 1954; Perrins, 1970; Hatchwell, 1991; Sydeman *et al.*, 1991), with earlier breeding associated with greater reproductive output. There are two key mechanisms likely responsible for this relationship (Verhulst and Nilsson, 2008). First, following favourable overwinter conditions, birds can breed earlier due to better individual state (Sorensen *et al.*, 2009), leading to enhanced reproductive investment. Secondly, in seasonal environments, earlier breeding is generally associated with a greater overlap with peaks in prey abundance (Stearns, 1992; Durant *et al.*, 2005). Such an effect may be particularly important in the North Sea, which is highly seasonal (Daan *et al.*, 1990), such that prey availability is heightened in earlier seasons. This is in line with Chapter 2, where I identified that within seasons, the proportion of 1+ group relative to 0 group lesser sandeel *Ammodytes marinus* (*hereafter* sandeel) diminishes as the season progresses. Globally, the majority of

seabird species are not advancing their phenology and may encounter temporal decoupling with the availability of lower-trophic prey, with negative reproductive consequences (Durant *et al.*, 2007; Keogan *et al.*, 2018). However, the rapid advancement in the timing of breeding breeding observed in this population linked to the increase in breeding productivity over the study suggests that this population is currently tracking changes in the timing of peak prey availability or benefitting from expanding prey diversity (chapters 2 and 3) in years when sandeel abundance is low. Crucially, the rapid advancement in breeding phenology recorded over the study appears to be a key factor linked to the productivity trend observed. However, although there is clearly a strong effect of phenology on productivity, the timing of breeding is likely to be a proximate driver, with the ultimate mechanism related to some unmeasured environmental factor, such as prey timing/abundance or fine scale weather conditions.

Winter climatic conditions adversley affect seabird survival (Grosbois and Thompson, 2005; Genovart *et al.*, 2013; Jenouvrier *et al.*, 2018). Indeed, in this population, stronger onshore winds are associated with increased mortality (Frederiksen *et al.*, 2008). Furthermore, foraging time among surviving individuals is higher during onshore winds in this species, suggesting that such conditions are challenging for shags (Daunt *et al.*, 2006, 2014). However, in this study, and contrary to expectation, high February Onshore Component, my index of severity in wind conditions, was associated with increased productivity. As demographic performance varies substantially between individuals, heterogeneity in climate-mediated individual responses may lead to changes in population structure and, in turn, average demographic rates (Coulson *et al.*, 2001; Benton, Plaistow and Coulson, 2006). Thus, one possible explanation for the positive effect of February Onshore Component is that individuals of different age or higher intrinsic quality may have higher survival probability during poor winter weather. This differential survival probability could then lead to higher average breeding success (Aebischer, 1986; Aebischer and Wanless, 1992; Grosbois and Thompson, 2005). Alternatively, surviving individuals may experience reduced competition for nest sites and food, with positive effects on productivity. However, without information on the

demographic structure of this population it is not possible to test the mechanisms underpinning this positive effect of February Onshore Component. Further, as the trend in February Onshore Component was decreasing, this variable explained interannual variation around the productivity trend, as opposed to the trend itself.

Prey availability during breeding is a key determinant of reproductive output in seabirds (Pierotti and Annett, 1990; Lewis, Wanless, *et al.*, 2001; Hilton *et al.*, 2015). Thus, the lack of an effect of SST and lagged SST, my proxies of sandeel availability, on productivity is in contrast to other studies in this population (Frederiksen, Harris, *et al.*, 2004; Burthe *et al.*, 2012) and other North Sea seabird species (Carroll *et al.*, 2015). However, there was evidence for a positive effect of the proportion of sandeel in the diet on productivity between 1985-2016 (the span of years over which the effect of this variable was tested). This effect was only apparent following detrending, which is potentially due to the increase in statistical power resulting from the considerable decrease in model residual variance when the fixed year effect was included in the model. Sandeel were traditionally considered one of the most profitable prey in the North Sea (Hislop, Harris and Smith, 1991), but climate-mediated reductions in the size, quality and availability of this species have been recorded over the past three decades (Wanless *et al.* 2004, 2005, Frederiksen *et al.* 2013; chapter 2). However, over the same period the diet of shags in this population has diversified, with the positive effect of sandeel suggesting that these alternative prey are less profitable. However, without independent data on prey capture rates or calorific content, it is not possible to ascertain whether the underlying mechanisms relate to sandeel, other prey types or both. It should also be noted that in the supplementary analysis, the proportion of sandeel in the diet was not an important determinant of breeding success. This disparity between the two breeding productivity variables may be due to brood size, which only incorporates nests with chicks present, being more sensitive to diet-mediated chick growth/survival rates, than those included in breeding success, which will also be sensitive to effects operating during incubation. However, as the proportion of sandeel in the diet reduced between 1985-2016, the positive effect does not appear

to be driving the overall increase in productivity, but the interannual variation around the long-term trend.

No other effects were found to be an important determinant of productivity in the main analysis. However, a positive effect of laying date in the previous year was identified as a determinant of breeding success, but only following detrending in the supplementary analysis. This link indicated that the effect of laying date in the previous year was only detectable once a fixed effect of year reduced the residual variance in the model, increasing statistical power to detect correlated effects. The direction of this effect suggests that following a later season the previous year, breeding success is higher. A lagged effect of previous laying date on breeding success may relate to reduced reproductive output in late years, allowing individuals to complete breeding in a better condition and breed earlier the following season. However, this effect is an opposite direction than would have been expected given the negative relationship between lagged productivity and current phenology in both the main and supplementary analyses, the effect of which received substantial support. Given that the effect of current phenology far outweighs the effect of lagged phenology in both productivity analyses, I consider the former to be of greatest significance to the demographic trends observed in this population.

Explanatory covariates of phenology

Temperature is a widely reported driver of avian breeding phenology, either directly as a cue (Visser, Holleman and Caro, 2009; Schaper *et al.*, 2012) or indirectly through bottom up impacts on resource availability (Durant, Anker-Nilssen and Stenseth, 2003; Both *et al.*, 2009; Burger *et al.*, 2012). My results accord with other studies in this species that have identified an effect of local climatic conditions on shag phenology (Frederiksen, Harris, *et al.*, 2004; Alvarez and Pajuelo, 2011). However, I report the first evidence of an effect of both current and lagged SST on the timing of reproduction in this species.

The negative impact of SST on phenology (i.e. breeding was early in years with high SST) may be due to an effect of water temperature on shag physiology (Enstipp *et al.*, 2007; White *et al.*, 2014). Late winter body condition is a key determinant of

seabird breeding phenology, with birds in better condition breeding earlier (Chambers *et al.*, 2009; Sorensen *et al.*, 2009). Thus, the effect of current SST could be operating via a constraint, such that in cooler temperatures, average individual condition may be reduced, leading to later breeding of the population. A negative effect, could also arise because of the effect of temperature prey availability during the energetically challenging winter months (Daunt *et al.* 2006, 2014; Chapter 3). This accords with Sorensen *et al.* (2009) who demonstrated that pre-breeding diet quality determines breeding phenology and subsequent success in Cassin's auklets *Ptychoramphus aleuticus*. Thus, temperature-mediated impacts on sandeel emergence (i.e. earlier emergence in warmer temperatures; Winslade 1974) or abundance of non-sandeel prey (Hiddink and ter Hofstede, 2008; ter Hofstede, Hiddink and Rijnsdorp, 2010), may alter prey availability during the non-breeding period. Linked changes in shag diet composition and pre-breeding condition, may alter breeding phenology, as suggested by Frederiksen *et al.* (2004). Crucially, I identified pronounced dietary changes during the non-breeding period in chapter 3, including a marked reduction in sandeel frequency and a concurrent dietary diversification, which could also be important determinants of shag breeding phenology, but due to sporadic sampling, it was not possible to include these data in the current analysis. An alternative mechanism is that in order to match breeding with peak prey availability, notably sandeel, shags in this population may utilise late winter conditions (i.e. SST) as a cue of prey scheduling. However, without independent data on the phenology/availability of multiple prey prior to and during the breeding period, and shag condition, it is not possible to ascertain whether the effect of current SST on breeding phenology is a constraint, a cue or both. The negative effect of current SST was removed from the best supported models of phenology in the detrended analysis, indicating that the effect of this variable should be treated with caution and it is unclear whether this effect is indeed important.

The positive effect of lagged SST on breeding phenology could also be linked to sandeel availability during the pre-breeding period, due to the bottom-up effects of temperature on sandeel recruitment in the previous year (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009). Following warmer temperatures in the previous year,

reduced sandeel recruitment may lead to depressed prey availability prior to breeding, resulting in a delay in shag breeding phenology. Although both current and lagged SST are important determinants of phenology, only the effect of current SST appears to be driving the trend, as the trend in this variable is in the direction consistent with the effect size in the explanatory model, whereas the trend in lagged SST explains interannual variation around the mean.

I identified a positive, lagged effect of past breeding on phenology in this population, with higher productivity in the previous year associated with earlier subsequent phenology. As seabird productivity is an integrated measure of environmental conditions (Frederiksen, Mavor and Wanless, 2007), higher productivity in the previous year likely represents favourable breeding conditions. Under such conditions, shags may complete breeding in better condition, which is carried over the non-breeding period and results in earlier breeding the following season. This interpretation is supported by the strong temporal autocorrelation in environmental conditions, as identified in the autoregressive analysis of breeding productivity and phenology and explanatory covariates, indicating interannual or cross-seasonal similarities in environmental conditions, which may also be a contributory factor to the demographic trends observed. Crucially, the effect of previous productivity on phenology remains in the best supported model following detrending, indicating that the observed effect is not due to concurrent trends in these two variables. Irrespective of the mechanism, my results suggest that the positive, lagged effect of previous reproduction is linked to the observed trend in breeding phenology. However, without individual data on body condition between years, it is not possible to ascertain whether this population level effect is due to lagged effects on condition, among year similarity in environmental conditions, or both.

The lack of an effect of breading season weather conditions on productivity and February weather conditions on phenology respectively is somewhat surprising, as breeding biology is often sensitive to prevailing, local conditions (Clutton-Brock, 1988; Velando, Ortega-Ruano and Freire, 1999; Boersma and Rebstock, 2014). Shag foraging behaviour is also strongly affected by wind (Daunt *et al.*, 2014; Lewis *et al.*,

2015; Kogure *et al.*, 2016). However, shags may have sufficient time and energy in order to increase foraging effort in response to challenging conditions, which may buffer productivity/phenology to these challenging conditions (Enstipp *et al.*, 2010; Lewis *et al.*, 2015). Further, the negative impacts of weather conditions on summer breeding is generally due to extreme events (Aebischer 1993; Newell et al 2015). Such effects may be comparatively rare and difficult to test for when mean weather variables are considered as continuous variables, as I did here, not as thresholds (Bateman, Vanderwal and Johnson, 2012). Further, no effect of population size was identified in the analysis of phenology or productivity. However, in the supplementary analysis of phenology, where the response variable modelled was laying date, there was evidence that laying was later at larger population sizes. In contrast to this, theory predicts that breeding should be earlier at larger population sizes (the Fraser Darling effect; Darling 1938), due to factors such as increased social stimuli, predator reduction and enhanced foraging efficiency (Coulson, 2002; Votier *et al.*, 2009). In support of this theory, Northern gannet *Morus bassanus* breeding phenology has advanced in the eastern Atlantic (Wanless *et al.*, 2008), over a period of marked population increases in this species (Mitchell *et al.*, 2004). Negative density dependent effects may also occur, through competition for nests sites or foraging habitats. However, population size was removed as a determinant of laying date following detrending, suggesting that this effect may be due to parallel trends with a third unmeasured variable which also shows a trend over time, and should be treated with caution. This may explain the disparity between the main and supplementary analyses. For example, the population size fluctuated dramatically over the entire dataset, but displayed a pronounced reduction in between 1986 and 2016, potentially leading to a spurious correlation with laying date. Given that population size was not an important determinant of phenology in the main analysis and was removed following the detrending analysis of laying date, this variable appears to be of limited significance in explaining breeding phenology or productivity in this population.

Conclusions and Implications

Productivity is a key demographic rate in marine top predator populations, reflecting prey availability, the abundance of lower trophic levels and prevailing abiotic conditions (Frederiksen, Mavor and Wanless, 2007). In this analysis, I have demonstrated that the effect of breeding phenology on productivity far outweighs any direct effects of current conditions (weather, population density and prey). Further, generally, ocean warming correlates negatively with seabird productivity, principally via bottom up climate mediated effects on prey availability (Barbraud *et al.*, 2012; Sandvik, Erikstad and Sæther, 2012; Hilton *et al.*, 2015; Sydeman *et al.*, 2015). However, productivity is actually increasing in this population, due to the effects of current SST on breeding phenology and conditions in the previous season, as indicated by lagged productivity. Combined, this study highlights the importance of understanding the determinants of breeding phenology in analyses of marine top predator reproduction, in addition to those immediately experienced during breeding. The breeding population size at this colony has fluctuated dramatically throughout the study (max in 1987: 1916 pairs; min in 1999: 259 pairs), declining markedly over the last 30 years, primarily due to periodic mass mortality events associated with stochastic extreme weather (Frederiksen *et al.*, 2008). Thus, although productivity is higher following poor winter weather, and has increased overall, this does not appear to be buffering this population to current, climate-mediated, environmental change effects on over-wintering survival. Frederiksen et al. (2008) demonstrated that there is a negative effect of extreme winter weather on immature and adult age classes. Over the period of increase in breeding success, there have been several winters in which survival rates were reduced in association with poor weather, notably 1998-99, 2004-05 and 2012-13. Thus, it would appear that the greater number of offspring being raised is not sufficient to compensate for these winters of high immature and adult mortality. As such, any increases in productivity may not be reflected in an increase in population size at this colony. Crucially, the frequency and severity of these extreme weather events are predicted to increase (IPCC, 2014). Future studies should aim to develop population models, incorporating the demographic rates and associated determinants identified in this

chapter, in order to test to what extent the increased productivity may provide sufficient resilience to predicted future environmental change.

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Chapter 5: Around the island: Long-term trends in nest distribution in a colonially breeding species in relation to reproductive success

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ABSTRACT

Changes in environmental conditions are altering animal species distributions throughout the globe. Most research has investigated these distributional trends over broad spatial scales. However, much less is known regarding fine-scale distributional shifts. Colonial breeding is a widespread phenomenon in the natural world. Although individuals breeding within the same colony will experience substantial commonality in environmental conditions, individual nesting locations within a colony may experience pronounced differences in physical characteristics or microclimate. Crucially, these differences could have a strong effect on within-colony variation in reproductive performance. However, few studies have quantified fine scale distribution and its relationships with breeding success, and to my knowledge none have investigated long-term changes in distribution in relation to breeding success. Here, I test for long-term changes in within-colony breeding distribution and the associated reproductive consequences in a population of European shags *Phalacrocorax aristotelis* breeding on the Isle of May, Scotland over two decades. At this colony, nests are distributed on both sides of a pronounced north-west/south-east island axis. The prevailing weather direction is westerly, meaning that those nests that are located to the west of the island axis are more exposed to wind conditions on average. I identified striking temporal trends in mean nest distribution, with a reduction in the proportion of nests located on the western side of the island axis over the course of the study, from 0.44 in 1994 to 0.28 in 2015. Over the same period, breeding success increased overall. Breeding success was consistently higher on the east of the island, and showed a more pronounced increase over time than the west (East: 0.72 chicks nest $^{-1}$ to 1.80; West: 0.66 chicks nest $^{-1}$ to 1.48 chicks nest $^{-1}$). However, I only found limited evidence that the increase in breeding success was related to patterns of change in distribution, with changes in phenology a more important driver. Given the predicted future changes in climatic variability in the region, the pronounced distributional changes observed may have important reproductive implications in this population, although effects will vary in relation to the prevailing direction of weather events.

INTRODUCTION

A central aim of ecology is to quantify the spatial distribution of animal populations, in order to establish the extrinsic drivers of population dynamics and change (Levin, 1992). Due to a range of environmental perturbations, the distribution of many species is changing throughout the globe (Thomas and Lennon, 1999; Wilson *et al.*, 2004). Much of the research has focused on distribution at broad spatial scales (at continental or regional levels), particularly in response to ongoing climatic change (Parmesan and Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006; Thomas, 2010; Chen *et al.*, 2011). However, at much smaller scales (millimetres to hundreds of metres), conditions can vary substantially due to factors such as microclimate, topography and resource availability, with profound implications for population processes (Fretwell and Lucas, 1969; Suggitt *et al.*, 2011). For example, microclimatic conditions on different sides of the same rock determine heat stress in limpets, aspect determines skipper *Hesperia comma* abundance on grassland hillsides and fine-scale microclimatic conditions determine temporal trends in carabid beetle assemblages (Seabra *et al.*, 2011; Lawson *et al.*, 2014; Park *et al.*, 2017). However, to date, few studies have investigated long-term changes in fine-scale distribution within populations, and consequences on demographic rates (Ackerly *et al.*, 2010).

Colonial breeding, whereby individuals aggregate with conspecifics for reproduction, is a widespread phenomenon in wild animals (Danchin, Boulinier and Massot, 1998; Krause and Ruxton, 2002). At the colony scale, individuals may experience substantial commonality in environmental conditions, such as broad-scale climate or resource availability. However, within colonies environmental conditions may vary over smaller spatial scales, due to differences in site-specific physical characteristics, such as height, aspect, exposure or slope (Lack, 1968; Clark and Shutler, 1999; Jones, 2001). Crucially, this small-scale variation may be a key determinant of reproductive output (Lack, 1968; Aebischer and Coulson, 1990; Kokko, Harris and Wanless, 2004). For example, greater vegetation cover reduces egg predation rates in Magellanic Penguins *Spheniscus magellanicus*, steeper nest ledge slopes increase failure rates in common guillemots *Uria aalge*, and higher nests are

more successful in lesser kestrels *Falco naumanni* (Negro and Hiraldo, 1993; Harris *et al.*, 1997; Stokes and Boersma, 1998). The physical characteristics of breeding locations may be relatively consistent over time (Robertson, 1985), and such locations may be used repeatedly over many years (Krohn, 1992; Kokko, Harris and Wanless, 2004). However, interannual variability and/or trends in environmental conditions, conspecific attraction or individual experience, may cause fine-scale changes in breeding distribution at colonies between years (Boulinier and Danchin, 1997; Boulinier *et al.*, 2008; Robert *et al.*, 2014). Such variation in local-scale breeding distribution may therefore be a key determinant of trends in reproductive output arising from the relative success of different breeding locations within the colony. However, to my knowledge no study has quantified temporal trends in fine-scale distribution within a breeding colony and the associated consequences on reproductive performance.

Using a dataset collected over two decades (1994–2015) I tested for long-term trends in fine-scale nest distribution and associated reproductive consequences in a colonially breeding species. The study was conducted at a breeding colony of European shags *Phalacrocorax aristotelis* (hereafter shag) on the Isle of May, southeast Scotland. The shag is a colonially breeding seabird endemic to the rocky coasts of the north-east Atlantic and Mediterranean (Wanless and M. P. Harris, 1997). Shags on the Isle of May breed in sub-colony aggregations that are distributed along the island coastline on visible, rocky ledges close to the shore, making them particularly amenable to quantify nest distribution (Aebischer, 1985; Barlow *et al.*, 2013). Further, the island lies on a north-west to south-east axis (Figure 19), with nests distributed on both the north-east and south-west sides. Shag productivity is susceptible to extreme wind conditions (Aebischer 1993; Newell et al 2015) and, as the prevailing weather direction at the colony is westerly, nests located on the south-west side of the island are more exposed to poor weather events on average. A consequence is that any long-term trends in the relative distribution of nests on either side of the axis could potentially have important implications for reproductive output due to changes in average wind exposure. At northern latitudes, the frequency and severity of extreme weather events is predicted to increase in the future (McInnes, Erwin and Bathols, 2011; Young, Zieger and Babanin, 2011; IPCC,

2014). The implications on future reproductive success of these predicted changes for shags breeding at this colony are therefore likely to depend on the locations of breeding birds relative to prevailing weather conditions. Crucially, I have shown that breeding success in this population has improved over the last two decades (Chapter 4), linked to the impacts of climate and lagged effects on breeding phenology. My analyses in Chapter 4 aimed to identify larger scale drivers of this change, while here my objective was to test whether changes in fine-scale distribution may have also contributed to this increase. Specifically, I tested if north-east facing nests, being less exposed to wind, have higher average breeding success than south-west facing nests, and whether the relative proportion of nests facing north-east has increased over time, which together could have resulted in the observed increase in average breeding success. My specific aims were therefore to:

a) quantify the number of years in which different areas were used and investigate interannual overlap in areas of usage;
b) test for temporal trends in nest distribution;
c) quantify whether breeding success and trends in breeding success differ between the south-west and north-east of the island; and
d) test whether changes in the relative proportion of nests on each side of the island axis are linked to the increase in population reproductive output that I have documented previously (Chapter 4).

METHODS

STUDY SITE

The study was conducted between 1994 and 2015 on the Isle of May National Nature Reserve, situated at the mouth of the Firth of Forth, southeast Scotland (56° 11'N, 02°33'W). The island lies on a pronounced north-west to south-east axis, characterised by steep vertical cliffs on the western face tapering to a rocky shoreline on the east (Figure 19). During the summer months, the island supports an internationally important breeding population of European shags *Phalacrocorax aristotelis* (hereafter shag; mean annual number of breeding pairs ± SD between 1994–2015: 509 ± 166; range: 259–968; http://jncc.defra.gov.uk/smp/). Shags

generally breed in clustered groups of nests (hereafter subcolonies) at suitable low-lying rocky ledges along the island perimeter. Breeding activity at nests was monitored regularly throughout the breeding season with the following states recorded, as appropriate: initial occupancy, nest building, presence of eggs, presence of chicks, number of chicks fledged (range: 0-4) and breeding failure. The location (latitude and longitude) of each nest was recorded using a handheld GPS (earth&OCEAN Technologies). In addition, each nest was also assigned as either south-west or north-east facing, based on the dominant axis of the island, which I hereafter refer to as nest aspect.

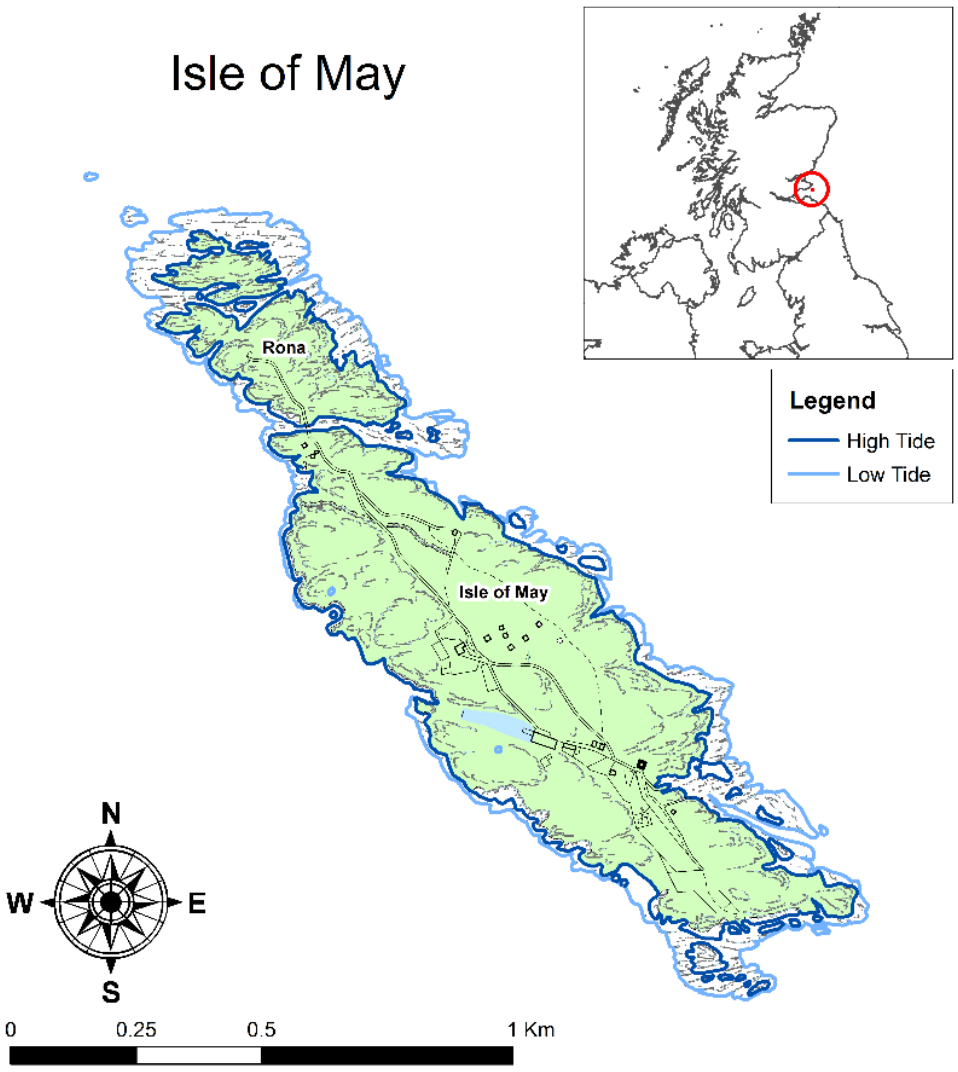

Figure 19 Map of the Isle of May plotted using the EDINA digimap service (http://digimap.edina.ac.uk/).

DATA MANIPULATION AND STATISTICAL ANALYSIS

All analysis was conducted in the 'R statistical programming language' (R Development Core Team, 2016). Plots were created in 'ggplot2' (Wickham, 2016).

In total, 13,532 records of breeding activity were observed. Repeated events at the same nest location in the same year (n = 235) were removed to avoid pseudoreplication, while 31 events were removed due to incomplete spatial data. Due to access difficulties at two locations, 484 events were also omitted. A further, 383 events where a bird had been observed, but no subsequent activity recorded, were also removed from the sample. However, in total these omitted events (n = 1133) represented 8% of all breeding records (n = 13,532) so I do not consider that their exclusion would influence my results (Table 16).

Of the retained sample size of 12,399 in which events were recorded, I focussed my analysis on those in which an egg had been laid (n = 11,133; hereafter "breeding events"), thereby excluding cases where some preliminary nesting activity was recorded, but no eggs laid (nest site occupancy: n = 271; nest building: n = 995; 10% of total sample size; mean ± SD annual number of nests with breeding activity but no laying: 58 ± 42; range: 13–197; Table 16). Of these breeding events, the final outcome (i.e. breeding success) of 140 events in which an egg was observed (mean annual number of events ± SD: 6 ± 21; range: 0–96) and 147 in which chicks were observed (mean annual number of events ± SD: 7 ± 26; range: 0–122) was unknown (n = 287; 2% of total sample size). An additional 17 events (0.15% of total sample size) failed after the egg/chick stage due to human disturbance (mean annual number of disturbed events ± SD: 1 ± 2; range: 0–7). Thus, the total number of nests in which laying had been confirmed and the breeding success was known was 10,829, and these data were used in analyses of reproductive output.

Table 16 Annual counts of all recorded events (some site occupancy was observed), breeding events (eggs or chicks observed), preliminary nesting activity (nest site occupancy, nest building) and annual mean breeding success (chicks $nest^{-1}$). Percentage of total nests recorded in each year is presented in parenthesis.

Year	Total	Breeding events (%)	Nesting activity (%)	Breeding success
1994	402	338 (84%)	64 (16%)	0.75
1995	577	524 (91%)	53 (9%)	1.07
1996	533	486 (91%)	47 (9%)	1.28
1997	640	576 (90%)	64 (10%)	0.94
1998	735	618 (84%)	117 (16%)	1.02
1999	368	259 (70%)	109 (30%)	0.58
2000	677	607 (90%)	70 (10%)	1.45
2001	712	659 (93%)	53 (7%)	1.76
2002	755	693 (92%)	62 (8%)	1.65
2003	1022	958 (94%)	64 (6%)	1.55
2004	797	600 (75%)	197 (25%)	0.43
2005	404	325 (80%)	79 (20%)	0.55
2006	567	535 (94%)	32 (6%)	1.56
2007	416	393 (94%)	23 (6%)	1.20
2008	414	401 (97%)	13 (3%)	2.00
2009	441	424 (96%)	17 (4%)	2.09
2010	510	472 (93%)	38 (7%)	2.11
2011	606	562 (93%)	44 (7%)	1.73
2012	705	645 (91%)	60 (9%)	1.47
2013	349	319 (91%)	30 (9%)	1.55
2014	380	364 (96%)	16 (4%)	1.90
2015	389	375 (96%)	14 (4%)	2.19

I conducted a supplementary analysis to investigate whether my results differed if I included both breeding events and those in which preliminary nesting activity was recorded (hereafter referred to as all nesting events). Results were comparable between analyses, so I present the analysis based on breeding events in the main text and the analysis based on all nesting events in Appendix 4.1 (Table A1–A2; Figure A1–A2).

Spatial analysis

I used different statistical techniques to address each of my research aims. To quantify the number of years in which different areas were used and investigate interannual overlap in areas of usage (aim a), I calculated Kernel Density Estimates and Bhattacharyya's affinity measure. I analysed changes in spatial distribution (aim

b) by quantifying trends in mean nest location using circular Linear Models (LMs) and in the relative proportion of nests on the south-west and north-east of the island axis using binomial Generalised Linear Mixed Models (GLMMs). To quantify whether average breeding success and trends in breeding success differed between the south-west and north-east of the island (aim c), I modelled nest-level breeding success using binomial GLMMs. To test whether changes in the relative proportion of nests on each side of the island axis was linked to population reproductive output (aim d), I modelled population-level breeding success using binomial GLMMs.

Utilisation distributions

To quantify the number of years in which different areas were used (aim a) I calculated Kernel Density Estimates (KDE; Calenge 2007) using a fixed bivariate-normal kernel estimator using the 'kernUD' function in the 'adehabitat' package (Calenge, 2006). For each year the core breeding area (50%) and area of active breeding use (95%; Ford and Krumme 1979) was estimated for all breeding events. Irresolvable convergence issues occurred when attempting to estimate the smoothing parameter (*h*) using the Least Squared Cross Validation (LSCV) caused by clustering of nest locations (Gitzen, Millspaugh and Kernohan, 2006). Thus, *h* was estimated by sampling 1,000 equally spaced points around the island perimeter and applying a small amount of random noise to each point using the 'Jitter' function in the 'base' package (R Development Core Team, 2016). Using this method, *h* was estimated as 15 m, with additional visual examination of utilisation distributions used to identify the bandwidth (Wade *et al.*, 2014). Core (50% kernel contour) and active (95% kernel contour) areas were then calculated for each year. To assess the long-term overlap of breeding areas, the 50% and 95% kernel contours were converted into grids with 1 m^2 cell size and the total number of years in which each grid cell was used was determined. The resulting data was then plotted using a British National Grid projection. To quantify interannual overlap between each of the annual estimated utilisation distributions of core area usage (50%), Bhattacharyya's affinity measure (Fieberg and Kochanny, 2005) was calculated using the 'kerneloverlap' function in the 'adehabitat' package to assess pairwise overlap across all years.

TRENDS IN DISTANCE ALONG COASTLINE AND ASPECT

To quantify temporal trends in fine-scale, within-colony distributions (aim b), I utilised the unique nest site location (latitude and longitude) data associated with each breeding event. Analysis of spatial Poisson Point Processes is increasingly used in analysis of animal distributions (Velázquez *et al.*, 2016), but such analyses require availability of suitable habitat to be spatially homogenous throughout the two dimensional landscape. This assumption was violated by my data, since nests on the Isle of May are clustered along the coastline, with nesting habitat unavailable in the central part of the island or beyond the shore. Therefore, temporal trends in breeding distribution were quantified using a 1D framework. I extracted the Ordinance Survey mean high water mark from The EDINA Digimap® service (http://digimap.edina.ac.uk/), which I used as the island perimeter. I connected two tidally separated islands (Isle of May and Rona; Figure 19; Figure 20a) using 'ArcGIS' (ESRI 2016), to ensure the island perimeter was a continuous feature. Next, each nest (Figure 20b) was snapped to the nearest point on the island perimeter (Figure 20c, Figure 20d). Although all breeding events were retained in the analysis of nest distribution, the total number of unique nest locations was reduced from 2420 to 1973 (mean annual number of snapped locations ± SD: 580 ± 185; range: 346–1051). This was for two reasons. First, in a subset of cases, nests snapped to the same point due to the irregular shape of the island perimeter, which includes convex and concave featuresincluding headlands (Figure 20c). Second, some nests snapped to the same location due to the resolution of the island perimeter. The clockwise distance from the northernmost point to the snapped location was then calculated as a proxy of spatial location in one dimension (hereafter referred to as distance along coastline). For analysis, each distance was then converted to an angle (in radians) relative to the midpoint of all nest points using the following formula:

$$Angle\ (rad) = (2 \times \pi \times Distance\ Along\ Coastline \div Total\ Perimeter\ Length) - \pi$$

This step was necessary to account for the circular nature of the island perimeter and thus ensure that the start and end were adjacent to each other.

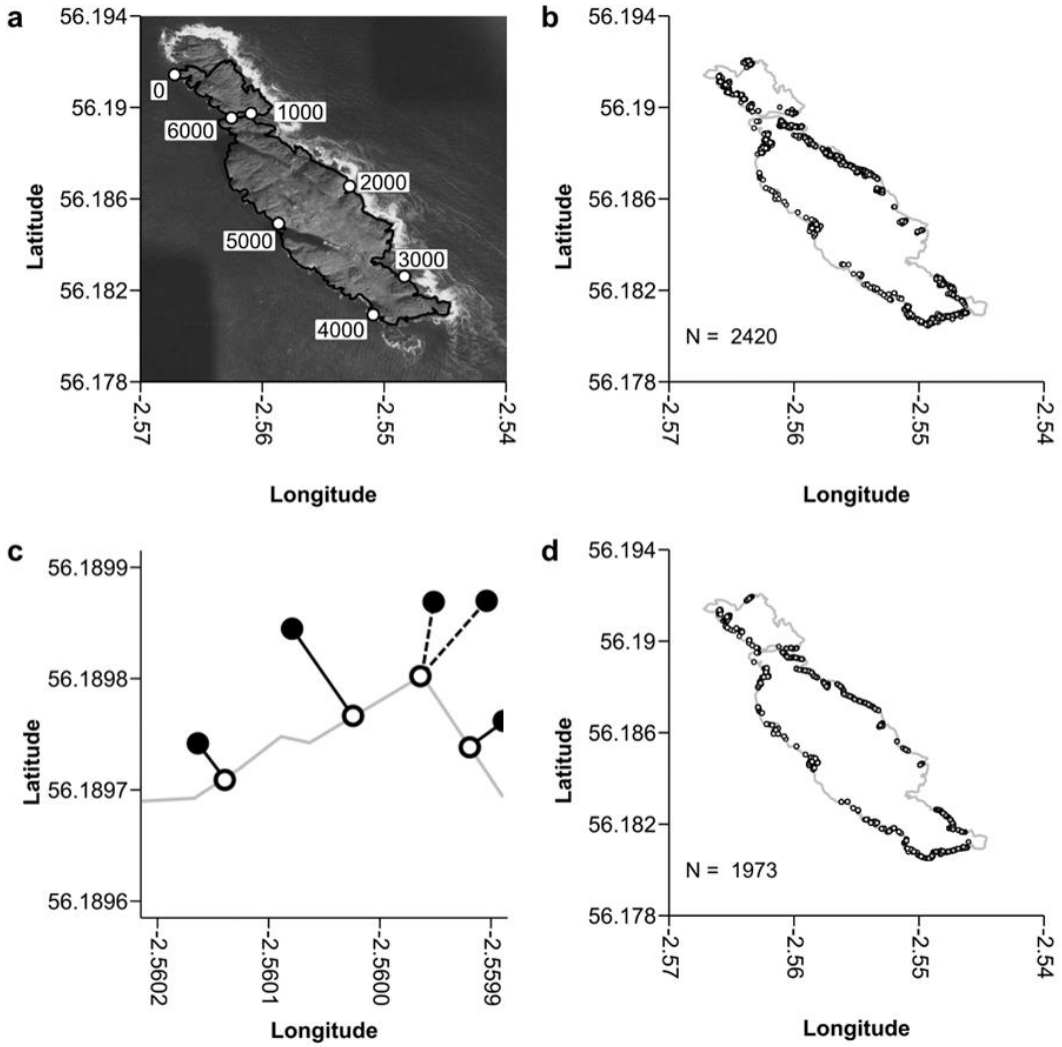

Figure 20 Aerial view of Isle of May displaying: a) satellite image with island high water mark boundary (solid black line); b) island boundary (grey line) with raw nest locations; and 1,000m marks (open circles) in a clockwise direction from the most north-westerly point; c) an example of nest snapping (solid lines indicate nests snapping to a single point; dashed lines indicate multiple points snapping to the same point); and d) snapped nest locations. Number of unique nest locations indicated with "N =" (a and d).

As hierarchical models are currently not available for circular data, temporal trends in annual mean nest distribution were quantified using the 'lm.circular' function from the 'Circstats' package (Lund and Agostinelli, 2012). To do this the annual mean direction (radians) of all breeding attempts was calculated using the 'circular.mean' function, from the same package. Trends in relative proportion of breeding events on either side of the central axis (i.e. annual number of nests on the south-west side of the island relative to all nests in that year; hereafter annual mean aspect) were quantified at the annual level by fitting binomial GLMMs with a logit-link function using the 'glmer' function in the 'lme4' package (Bates *et al.* 2015). Two models were fitted to both annual mean direction (radians) and annual mean aspect for all breeding events, including a model containing a fixed effect of year and a null, intercept only model. A random effect of year was also included in the model of annual mean aspect to account for overdispersion (Harrison, 2015), but was not required for the circular annual mean direction data, since these data cannot be overdispersed. To aid interpretation, I converted annual mean direction (radians) back to distance along coastline.

Trends in an covariates of breeding success

To quantify whether average breeding success and trends in breeding success differed between the south-west and north-east of the island (aim c), I adopted a binomial modelling approach for nest-level breeding success (hereafter nest breeding success; Cook *et al.*, 2014; Carroll *et al.*, 2015). This approach avoided predicted values being higher than the maximum number of chicks fledged in this population (four; Harris *et al.* 1994) or below zero. Thus, nest breeding success was modelled as the number of chicks fledged / 4. I fitted a binomial GLMM for nest breeding success, with fixed effects of year, nest aspect and a year by nest aspect interaction. Random effects of year and nest ID were fitted to account for pseudoreplication, while a breeding event-level overdispersion term was also included (Harrison, 2014).

To test whether the trend in annual breeding success identified in chapter 4 was related to the relative proportion of nests on each side of the island (aim d), I undertook an aggregate, annual-level analysis of breeding success (hereafter

population breeding success). In this instance I fitted a Binomial GLMM, where population breeding success was modelled as the total number of chicks raised annually / maximum number of chicks possible (number of nests in which egg laying occurred * 4). I included fixed effects of year and annual mean aspect. I also included the two determinants of population breeding success identified in chapter 4: February Onshore Component (hereafter February OC) and Median Laying Date (hereafter laying date). To do this I fitted a global model containing an effect of year, annual mean aspect, February OC and laying date, and a random effect of year to account for overdispersion. Ideally, I would also have tested the effects of nest-level phenology and environmental conditions (temperature, wind exposure, moisture) on nest breeding success, but nest-level data were not available for these variables.

To test for collinearity between covariates included in the annual analysis, I calculated Pearson's correlation coefficients. As year and annual mean aspect were highly correlated (R = -0.84), these two variables were not included in the same models (Appendix 4.2 Table A28).

A Poisson error structure could be a valid distribution for number of chicks fledged. Therefore, I undertook two further supplementary analyses, in which I fitted a GLMM with a Poisson error distribution to the model of nest breeding success in relation to year and nest aspect, and population breeding success in relation to year, annual mean aspect, February OC and laying date, with the latter also containing a log(number of nests year^{-1}) offset. An offset was not required in the Binomial analysis since the response variable incorporates the number of nests. Results were comparable between the two modelling approaches and thus I consider the use of binomial analyses appropriate. Binomial models are presented in the main text with Poisson models presented in Appendix 4.3 (Table A29).

In all analyses, model selection was performed on the global model for each response variable (annual distance along coastline, annual mean aspect, nest and population breeding success) using Akaike's Information Criterion corrected for small sample sizes (AICc), where the best model was considered to be that with the lowest AICc value. In each case all possible combinations of fixed effects included in the global model were fitted using the 'dredge' function in the 'MuMIn' package (Bartoń, 2016). Models within 2 AICc points were considered to have similar levels of support

(Burnham and Anderson, 2002), unless they contained additional parameters, in which case they were considered uninformative (Arnold, 2010). To avoid model convergence issues, the fixed effect of year was centred on zero (by subtracting mean year from each value) and rescaled (by dividing the centred value by the standard deviation of year). However, plots are presented on the original unadjusted scale.

RESULTS

SAMPLE SIZES AND OVERALL DISTRIBUTION

Over the study, core (50%) areas were associated with the north-east (~1000 m around perimeter from the most north-westerly point), east (~2000 m), southeast (~3000 m), and northwest (~6000 m; Figure 21). The mean annual pairwise overlap ± SD of core nesting areas (50%) for all breeding events was 0.73 ± 0.12 (range: 0.50–0.97; Bhattacharyya's affinity indices; Appendix 4.4 Table A30). Crucially, there was strong overlap between successive years (mean of successive years ± SD: 0.88 ± 0.05), but less overlap between years that were further apart (mean of all non-successive years ± SD: 0.71 ± 0.11).

The annual mean ± SD distance along coastline of breeding events was 2165 m ± 733 m (range: 1352–3251 m). The total number of breeding events on the south-west and north-east side of the island was 4807 (annual mean number of events ± SD: 95 ± 55; range: 109–442) and 7975 (annual mean number of events ± SD: 363 ± 106; range: 233–630), respectively. The annual mean proportion of breeding events ± SD on the south-west side of the island was 0.36 ± 0.06 (range: 0.26–0.45).

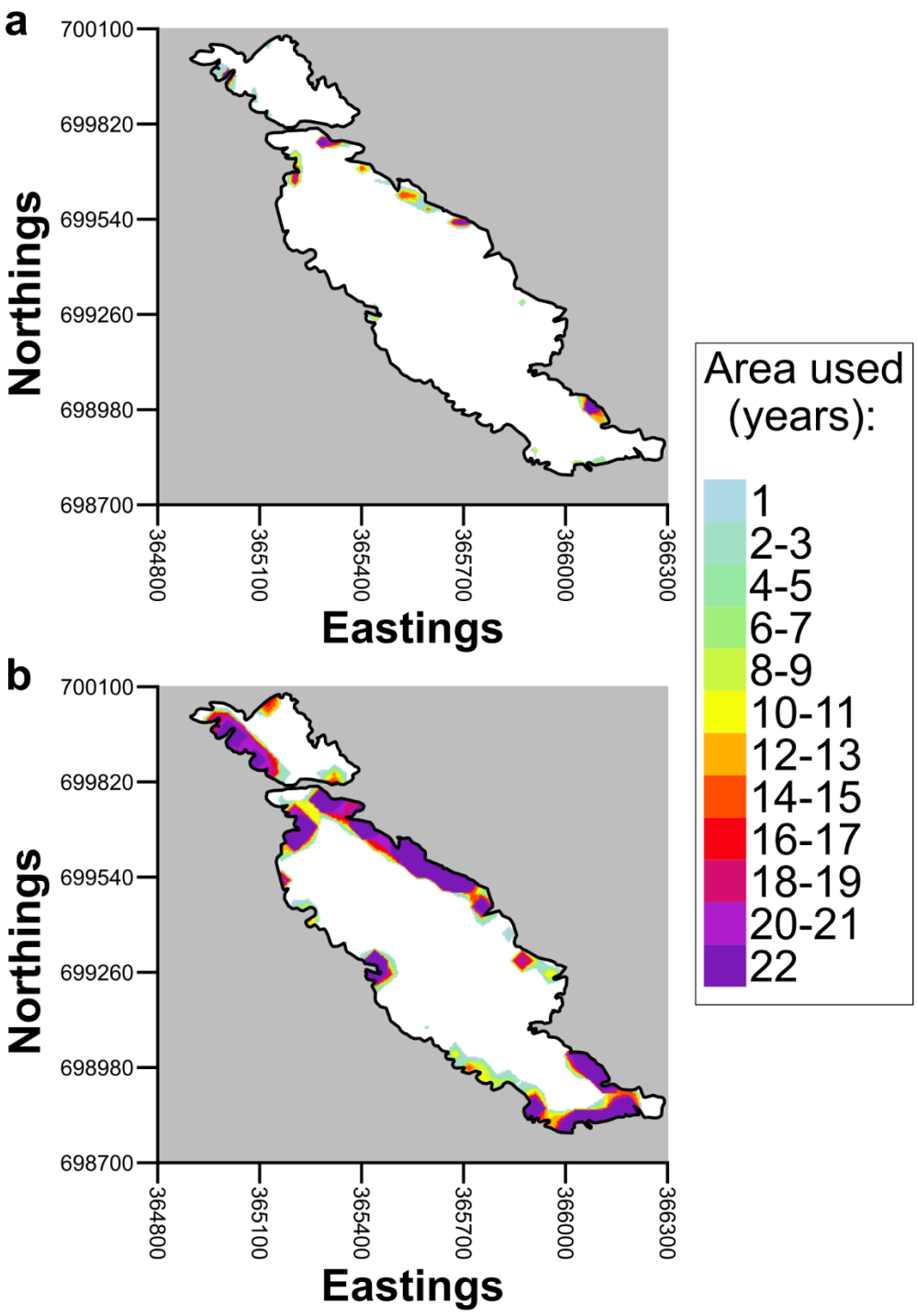

Figure 21 Overlap in nesting distribution within the a) core area (50%) and b) area of active use (95%) for all breeding events. Areas used indicates number of years core areas overlap between years.

TRENDS IN DISTANCE ALONG COASTLINE AND ANNUAL MEAN ASPECT

The annual mean distance along the coastline of breeding events showed a pronounced temporal trend from a predicted distance of 3123 m in 1994 to 1202 m in 2015 (Table 17; Figure 22a). Further, a decreasing proportion of events was located on the south-west of the island over the course of the study (annual mean aspect: 0.44 in 1994 and 0.28 in 2015; Table 17; Figure 22b, c).

Table 17 Model selection table for circular Linear Models testing for temporal trends in annual mean distance along coastline and binomial Generalised Linear Mixed Models for temporal trends in annual mean aspect for all breeding events. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z/t values, number of parameters (k), difference in AICc between top model and selected model (Δ AICc) and Akaike weight relative to other models (ω_i). Top models are shown in **bold**.

Response	Rank	Model	Est	SE	t/z	k	Δ AICc	ω_i
Distance along coastline	**1**	***Year***				**3**	**0.00**	**0.99**
		Year	**-0.30**	**0.05**	**-6.09**			
	2					1	25.43	0.01
Annual mean aspect	**1**	***Year***				**3**	**0.00**	**0.99**
		Year	**-0.22**	**0.03**	**-7.63**			
	2	*i*				2	25.13	0.01

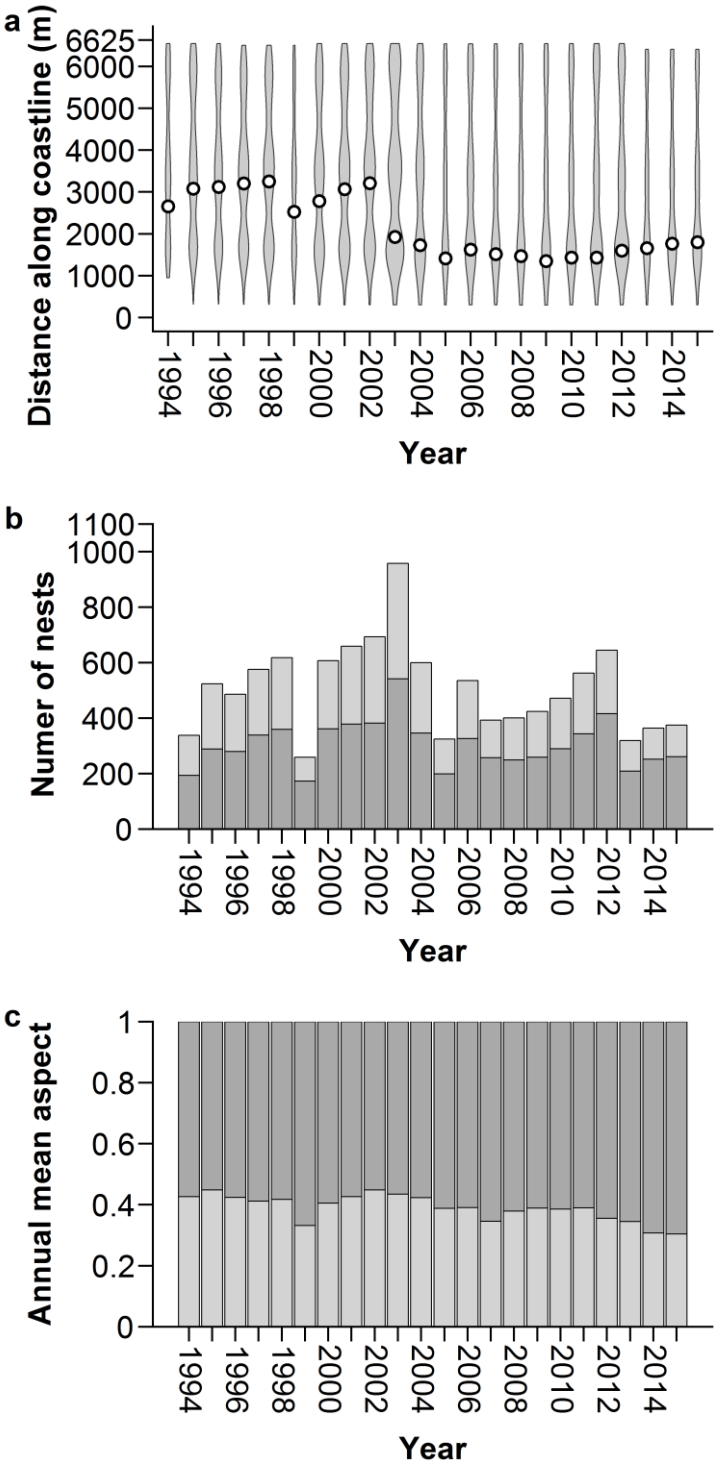

Figure 22 a) Violin plots displaying interannual variation in distance along coastline between 1994 and 2015 for all breeding events. The violin plot for each year is scaled relative to the sample size of nests. Annual circular mean indicated with open circles (○); b) interannual variation in number of nests on the south-west (light grey) and north-east (dark grey) side of the island between 1994 and 2015 for all breeding events; and c) interannual variation in the proportion of south-western (light-grey) and north-eastern nests (dark grey) between 1994 and 2015 for all breeding events.

TRENDS IN AND COVARIATES OF BREEDING SUCCESS

Across the study, the pooled mean of nest breeding success ± SD was 1.48 ± 1.18 (range: 0-4). The annual mean population breeding success ± SD across all years was 1.40 ± 0.53 chicks nest^{-1} (range: 0.43-2.18).

Breeding success was consistently higher at nests on the north-east side of the island than the south-west. In addition, nest breeding success increased over the study, with north-eastern nests displaying a more rapid increase than those in the south-west (SW: increase in breeding success from 0.66 chicks nest $^{-1}$ in 1994 to 1.48 chicks nest $^{-1}$ in 2015; NE: increase in breeding success from 0.72 chicks nest $^{-1}$ to 1.80 chicks nest $^{-1}$; Table 18; Figure 23).

Mean annual population breeding success was significantly correlated with annual mean aspect (Spearman's rho = -0.44; p = 0.043; Figure 24). However, the best-supported model for population breeding success contained only an effect of year and laying date (Table 18; extended model selection table presented in Appendix 4.4 Table A31). Breeding success increased from 0.98 in 1994 to 1.68 in 2015. However, median laying date had a negative effect, from 1.80 chicks nest^{-1} at the earliest median laying date (149th day of year; ~29th May) to 0.82 chicks nest^{-1} at the latest (98th day of year; ~8th April). A model containing a fixed effect of laying date only, received similar levels of support. A model containing a negative effect of both laying date and annual mean aspect was outside the 2 AICc points criteria for support, indicating weak evidence for an effect of annual mean aspect on population breeding success. In contrast to chapter 4, there was poor support for an effect of February OC.

Table 18 Model selection table Generalised Linear Mixed Models testing for temporal trends and effects of nest aspect on nest breeding success and for Binomial GLMMs testing for temporal trends and drivers of population breeding success. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z values, number of parameters (k), difference in AICc between top model and selected model (Δ AICc) and Akaike weight relative to other models (ω_i). Due to the large number of models, I only present those within 2 AICC points of the top model. Nest aspect presented as south-west (SW) relative to north-east of the island. Top models are shown in **bold**. Models with similar levels of support are indicated with †. February OC = February Onshore Component.

Response	Rank	Model	Est	SE	z	k	Δ AICc	ω_i
Nest breeding success	**1**	***Year + Nest aspect + Year*Nest aspect***				**5**	**0.00**	**0.8**
		Year	**0.37**	**0.12**	**3.13**			
		Nest aspect	**-0.21**	**0.04**	**-5.36**			
		Year*Nest aspect	**-0.06**	**0.03**	**-2.24**			
Population breeding success	**1**	***Year + Laying date***				**4**	**0.00**	**0.40**
		Year	**0.17**	**0.07**	**2.33**			
		Laying date	**-0.24**	**0.07**	**-3.30**			
	2	*Year + Feb OC + Laying date*				5	1.70	0.17
		Year	0.18	0.07	2.55			
		Feb OC	0.09	0.07	1.33			
		Laying date	-0.26	0.07	-3.62			
	3†	*Laying date*				3	1.80	0.16
		Laying date	-0.30	0.08	-3.87			

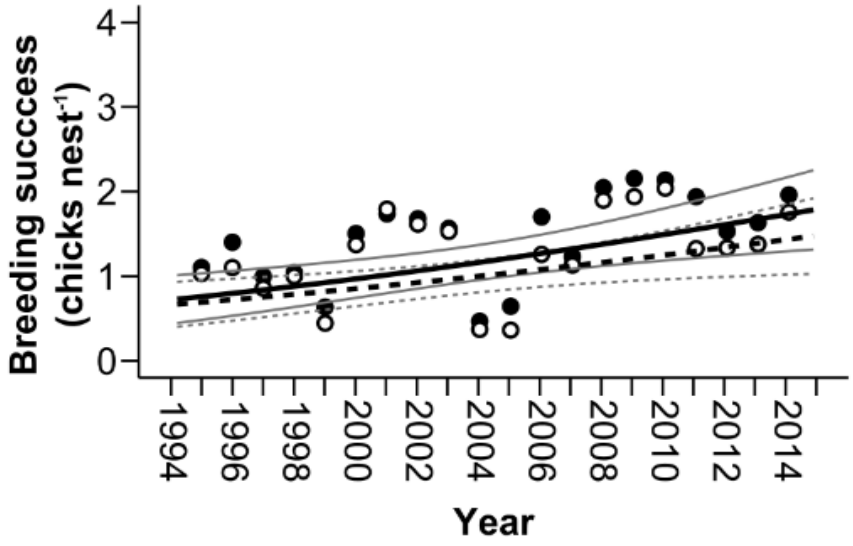

Figure 23 Annual mean values, predicted values and confidence intervals for temporal trends in nest breeding success (chicks nest^{-1}) on the south-west and north-east of the island between 1994 and 2015. Dashed line and hollow circles (○) indicate the south-west of the island. Solid line and filled circles (●) indicate north-east side of the island.

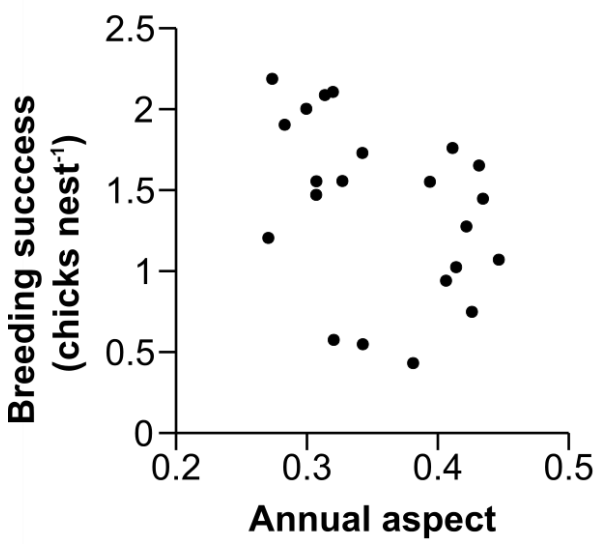

Figure 24 Relationship between annual breeding success (chicks nest^{-1}) and annual mean aspect (Speaman's Rho = -0.44; p = 0.043).

DISCUSSION

Using a 22-year dataset, comprising 11,133 individual breeding events from 2420 different nest sites, I quantified for the first time in a colonial breeding species the long-term temporal trends in fine-scale breeding distribution and associated reproductive consequences. Over this period, I identified striking temporal trends in breeding distribution whereby an increasing proportion of nests were located on the north-eastern side of the island over the course of the study. Throughout the colony, breeding success increased over the study, nests on the north-eastern side were more successful on average, and the increase in breeding success was more marked in this category. However, although annual population breeding success increased over the study, there was limited evidence that this was related to changes in the relative proportion of nests on different sides of the island axis. Overall, these results indicate pronounced distributional trends at this colony, which are important drivers of nest level reproductive output.

OVERALL DISTRIBUTION AND BREEDING SUCCESS

Although breeding events were recorded in many locations along the island perimeter, several areas of core use were identified over the study, some of which were occupied in all 22 years. Interannual overlap in core areas was generally high across the study (range: 0.50–0.97), suggesting that birds return to similar areas between successive years. Such overlap in areas of core use over the study is likely determined by many factors including site availability and quality, prevailing environmental conditions, individual experience, and conspecific attraction/competition (Danchin, Boulinier and Massot, 1998; Kokko, Harris and Wanless, 2004; Zador, Parrish and Punt, 2009; Robert *et al.*, 2014). European shags *Phalacrocorax aristotelis* (hereafter shag) preferentially choose nest sites of high physical quality (i.e. greater cover, better drainage, good visibility; Aebischer, 1985; Velando and Freire, 2003) and thus these areas of core usage may have favourable nest site characteristics. Further, following egg laying, the majority of breeding attempts are successful at this colony (percentage of successful nests among those in which eggs were laid over the course of the study: 7232 / 10,829 = 67%). Shags are

more likely to breed at the same nest the year following a successful breeding attempt (Aebischer, Potts and Coulson, 1995; Barlow *et al.*, 2013), which may lead to high consistency in area use between years. Shags also breed close to their natal location, and so strong philopatry could also be a contributory factor (Aebischer, Potts and Coulson, 1995; Barlow *et al.*, 2013). However, it should be noted that inter-annual, broad-scale breeding distribution can remain similar, even if finer scale distribution, such as nest occupancy and density, varies between years (Rebstock, Boersma and García-Borboroglu, 2016).

Overall, in line with areas of core use, the relative proportion of nests on the south-west of the island was consistently lower throughout the study. This preference for the north-east of the island is in contrast to Aebischer (1993), who found that in 1982, 59% of nests were located on the south-west. Shags in the UK generally nest on low-lying, rocky outcrops (Wanless and M. P. Harris, 1997), which are a feature of the north-western shores. One possible explanation for the difference in distribution observed in both studies is that the shag population was far higher during the 1980s (1980-1989: mean ± SD: 1456 ± 251; range: 1041-1916; http://jncc.defra.gov.uk/smp/) than over this study (mean ± SD: 509 ± 166; range: 259-968). If the north-east provides favourable breeding habitat then this area may become saturated at higher population sizes, with excess birds forced to nest on the less favourable south-western side. Pigeon Guillemots *Cepphus columba* breeding on Mitlenatch Island, British Columbia, also show a distributional preference, with the majority of birds nesting on the south of the island, possibly linked to the beneficial effects of sun exposure on nest temperature (Emms and Verbeek, 1989). An alternative explanation may be linked to a dramatic mortality event in the winter of 1993-94, when 85% of breeding adults died (Harris, Wanless and Elston, 1998). Although the event took place when birds were up to several hundred kilometres from the colony, it is possible that mortality was biased towards particular sub-colonies. Anecdotal evidence indicates that certain sub-colonies went extinct or were disproportionately depleted from 1994 onwards, in particular those in the south-west of the island (S. Wanless & M. Harris pers. comm.). However, we do not have the quantitative data on nest location spanning the mortality event to test this assertion. As natal philopatry is strong in shags (Aebischer, 1995; Barlow *et al.*, 2013),

high interannual recruitment to the areas in which the majority of birds nest (north-east of the island over this study) could also serve to perpetuate any changes in distribution. Attraction to successful conspecifics may also be important, particularly as this area is more successful on average. Irrespective of the mechanism, shags displayed an increasing preference for breeding on the north-east of the colony.

In line with this overall pattern of distribution, breeding success was consistently higher in the north-east of the island compared to the south-west. This effect could be indicative of more favourable physical characteristics or microclimatic conditions on the north-east of the island. For example, local-scale environmental conditions are believed to cause reproductive success to differ between little auk *Alle alle* subcolonies (Jakubas and Wojczulanis-Jakubas, 2011). On the Isle of May, prevailing westerly weather conditions have contrasting effects on the two sides of the island. For example, Aebischer (1993) showed that a strong westerly gale destroyed 49% of nests on the exposed south-west side of the island, compared to none on the north-east. The number of chicks fledged per pair was substantially lower on the south-west side of the island (-31%) following this event, due to nest desertion, greater hatching failure and reduced reproductive output in nests that relayed. Similarly, 15% of shag nests on the exposed south-west side of the island failed during a westerly storm in 2011, compared to none on the more sheltered north-east coast (Newell *et al.*, 2015). This study also reviewed past weather records and found that seven out of the eight strongest summer storms were westerly (Newell *et al.* 2015). Chronic, sub-lethal effects of weather conditions on parents could also be a factor, potentially leading to lower productivity on the more exposed south-west of the island and reduced over-wintering survival probability of adults breeding there due to carry-over effects of summer condition. Further, in Tufted Puffins *Fratercula cirrhata*, contrasting foraging locations and trophic-level of prey leads to subcolony differences in reproductive output (Hipfner, Charette and Blackburn, 2007). Indeed, shags in this population also display sub-colony segregation in foraging locations close to the colony (Bogdanova *et al.*, 2014). Such effects may determine foraging profitability on different sides of the Isle of May, potentially contributing to the link between nest distribution and breeding success. Occupancy of north-eastern nests by higher quality individuals could also account for

the heightened breeding success associated with these areas. For example, reproductive output in Yellow Legged Gulls *Larus michahellis* differs between vegetated and bare subcolonies, likely due to a combination of both individual quality (age) and habitat features (Oro, 2008). Whichever process underpins these patterns, there is a marked benefit to shags in this population of nesting on the north-eastern side of the island.

Trends in distance along coastline and annual mean aspect

The mean distance along coastline of all breeding events changed significantly over the study. At the same time, the annual mean aspect changed, such that fewer nests were located on the south-west of the island by the end of the study. This distributional change appeared to be driven by a reduction in the size of sub-colonies associated with the south-west of the island and a parallel increase in those on the north-east, rather than the establishment of new areas. Although shags display a tendency to breed relatively near to their natal site (mean: 464 ± 500 m; range: 0 to 1962 m; Barlow *et al.*, 2013), this is not universal and many individuals may recruit to nests many hundreds of metres away (Aebischer, Potts and Coulson, 1995; Barlow *et al.*, 2013). Similarly, although Black guillemots *Cepphus grylee* breeding of the island of Flatey, Iceland, tend to return to their natal site, there is a clear spatial preference, such that more birds recruit to the west than the east of the colony (Frederiksen and Petersen, 1999). In addition, adult shags regularly move nest location between breeding seasons (males: median 1.5m; females: 5.0 m; Aebischer, Potts and Coulson, 1995). Although the physical characteristics of individual nest sites/subcolony areas may remain largely consistent between years, the relative quality of different locations may change due to temporal variation in environment conditions, notably weather. For example, Bonter *et al.* (2014) demonstrated that optimal nesting locations change between years due to fluctuating weather conditions. Crucially, shags are known to display behavioural plasticity in breeding distribution, with individuals moving to better protected nests following American mink *Neovison vison* invasion (Barros *et al.*, 2016). These behaviours could result in a gradual change in nesting distribution of the population as a whole, if individuals are showing similar responses to changing environmental conditions. Shags are also

more likely to move nest sites following reproductive failure (Aebischer, Potts and Coulson, 1995). Thus, temporal changes in environmental conditions may have different effects across the colony depending on the relative orientation and exposure along the island axis, potentially leading to the observed distributional trends. Periodic, extreme weather events generally have a greater impact on the south-west of the island (Aebischer, 1993; Newell *et al.*, 2015). Following such events, poor recruitment in or higher average dispersal from failed areas may lead to distributional changes. Finally, although lesser sandeel *Ammodytes marinus* are predominantly associated with sandy habitats, the increasing proportion of non-sandeel prey in the diet (chapter 2 and 3) are associated with a wider range of habitats (Watanuki *et al.*, 2008; Heessen, Daan and Ellis, 2015). If certain areas of the colony provide access to foraging habitats associated with different prey (Christensen-Dalsgaard *et al.*, 2017; Michelot *et al.*, 2017), then the dietary trends observed in chapters 2 and 3, could also be driving the distributional trends.

Conspecific attraction to densely populated or successful areas is a key determinant of breeding distribution in many colonial breeding seabirds (Danchin, Boulinier and Massot, 1998; Boulinier *et al.*, 2008), particularly where habitat availability is patchy and nests are conspicuous. In shags and other colonially breeding species, first time breeders tend to recruit to previously successful/occupied areas (Snow, 1963; Aebischer, Potts and Coulson, 1995; Danchin, Boulinier and Massot, 1998; Frederiksen and Petersen, 1999). The distribution of experienced breeders can also be affected by conspecific performance (Schjørring, Bregnballe and Gregersen, 2000; Naves, Yves Monnat and Cam, 2006). For example, between years, black-legged kittiwakes *Rissa tridactyla* tend to emigrate from the previous year's least successful cliffs to those which are most successful (Danchin, Boulinier and Massot, 1998). Thus, the expansion of subcolonies associated with the north-east of the island may have arisen from birds being attracted to these relatively more successful areas and/or breeding dispersal from the relatively poorer south-west. Ultimately it is a combination of these extrinsic and intrinsic factors that will determine changes in breeding distribution, but without information on the fine-scale physical conditions or individual condition and dispersal

strategies between years, it is not possible to ascertain the underlying mechanisms driving the distributional trends observed.

Trends in and covariates of breeding success

Both nest and population breeding success increased over the study. In line with chapter 4, the best model for population breeding success contained an effect of both median laying date and year. As breeding success is an integrated measure of environmental conditions at all relevant scales (Frederiksen, Mavor and Wanless, 2007), the increase may be linked to more favourable climatic conditions or prey availability as a result of advancing phenology. In chapter 4, I also demonstrate that trends in SST and carry-over effects have led to increased productivity over the past five decades, mediated via advancing phenology. However, as nest-level phenology data were unavailable, it was not possible to quantify the effect of phenology on nest breeding success. However, the nest-level analysis demonstrated that the increase in breeding success was more rapid in the north-east. The mechanism for this is unclear, but may be due to emigration to the north-eastern shores by high quality birds, increasing average quality in this area, or enhanced nest site conditions on the north-east of the island owing to changing environmental conditions.

There was limited evidence that the relative proportion of nests on each side of the island was an important determinant of population breeding success. This is somewhat surprising as inclement weather is known to affect shag reproductive output (Velando, Ortega-Ruano and Freire, 1999), with disproportionate effects on either side of the island previously observed at this colony (Aebischer, 1993; Newell *et al.*, 2015). However, the ultimate driver is possibly linked to some unmeasured factor, such as fine-scale weather exposure, which would vary on a nest-by-nest basis, even within the same side of the island. Such effects may not accord closely with broad climatic variables, such as those I analysed in chapter 4. However, data on nest-level environmental conditions was not available and so an analysis of the drivers of fine scale breeding success was not possible. Another possible explanation is that even where nest sites are sheltered from such events due to differences in south-west/north-east exposure, individuals may be affected at their foraging locations. Although shags display foraging segregation at close and distant locations,

there is considerable overlap at intermediate distances, where the majority of foraging occurs (Bogdanova *et al.*, 2014). Thus, environmental change could affect birds breeding on both sides of the island similarly, over-riding any differences associated with nest distribution. Chapter 4 suggested that broad-scale, late winter/pre-laying conditions were more important determinants of population breeding success than current conditions, which may also be why no effect of annual mean aspect was detectable. However, I found no effect of February OC on population breeding success in this analysis. This is unsurprising, as in Chapter 4, I identified a pronounced negative trend in this variable over the past 30 years. As such, due to the generally lower values of February OC over this study, it may not be possible to detect an effect over this shorter range of years.

Implications and future directions

By incorporating the drivers of productivity identified in chapter 4 into this analysis of fine-scale breeding distribution, I have again demonstrated that at the population level, timing of breeding is a key determinant of breeding success in the population. However, my nest-level analysis suggests that there are fine-scale factors that also affect breeding success. Although I was unable to detect an effect of changes in nest aspect on population-level breeding success, it is possible that nest distribution affects breeding success via differences in timing of breeding on either side of the island, something I was unable to test. Given that the timing of breeding was the key determinant of productivity in both this chapter and chapter 4, a future priority is therefore to test the relationship between fine-scale breeding distribution and phenology.

In this study, I have identified a pronounced distributional trend, with a greater proportion of nests now on the north-east of the island than in the past. Over the same period reproductive output increased, more rapidly on the north-eastern shores. With a greater proportion of nests now on the north-east of the island, the vulnerability of this population to poor westerly weather may be diminished compared to the past. However, strong easterly gales can also affect shags in this population (Aebischer and Wanless, 1992), and may now have a more pronounced effect on population demography, but such events are rare during breeding (Newell

et al., 2015). Flight in shags is costly, with the direction of departure, prevailing wind and relative location of feeding grounds important determinants of shag foraging energetics (Kogure *et al.*, 2016; Hicks *et al.*, 2017). Thus, the distributional trends observed may alter shag flight behaviour or survival, since the relative position of different nests could alter adult energy expenditure during breeding and linked individual condition. Since shags occupy better quality sites with age (Aebischer, Potts and Coulson, 1995; Daunt *et al.*, 2007), it is also possible that low quality or young birds predominantly breed on the south-west of the island. Climatic events disproportionately affecting different areas of the island could therefore have implications for population age structure. Future analyses should aim to quantify spatial variation in sub-colony structure utilising recent advances in spatial statistical techniques such as INLA models (Bakka *et al.* 2018). This could allow the relationships between spatial distribution, environmental conditions, conspecific attraction and fitness to be analysed in a 2D framework, which may lead to a more mechanistic understanding of the processes driving changes in spatial distribution to be uncovered.

In summary, and in line with Chapter 4, shags in this population appear to be displaying flexible demographic responses, in terms of both spatial distribution and reproductive output, to ongoing environmental change in the North Sea. In doing so, shags breeding at this colony may have reduced their susceptibility to extreme weather events, which have occurred periodically over the past 2 decades, predominantly from a westerly direction. However, predicting any future consequences of sub-colony spatial structuring on population demography remains challenging, since impacts will depend upon both storm magnitude and direction relative to breeding distribution (Newell *et al.*, 2015). Finally, the trends in within-colony, spatial structuring uncovered in this chapter may further help our understanding of the ecological processes underpinning colonial living and the fine-scale mechanisms driving population dynamics in colonial species.

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Chapter 6: General discussion

SUMMARY

Human activities, including climate change and overfishing, are having rapid, pervasive and deleterious impacts on marine ecosystems across the globe (Worm *et al.*, 2006; Halpern, 2009; Hoegh-Guldberg and Bruno, 2010; Poloczanska *et al.*, 2013). Due to the tight coupling between lower trophic levels and climate, pronounced changes have been observed in many planktonic and forage fish populations (Hays, Richardson and Robinson, 2005; Perry *et al.*, 2005), many of which are an important dietary component for a guild of marine top predators, including seabirds (Cushing, 1990; Cury *et al.*, 2000). Globally, many seabird populations are in decline (Croxall *et al.*, 2012; Paleczny *et al.*, 2015). Implicated in these declines are numerous factors, including climate-mediated environmental change, introduced predators and competition with fisheries (Halpern, 2009). However, owing to the vastness and inherent variability of the oceans, quantifying the links between these perturbations and higher-tropic marine organisms such as seabirds is a challenge. Thus, the mechanisms underpinning these changes remain poorly understood. In recent decades a suite of technological and statistical advancements have provided novel insights into the mechanisms underpinning seabird demography (Grémillet and Boulinier, 2009). However, traditional techniques, such as long-term monitoring of seabird diet and demography, are indispensable, and remain a crucial tool through which to monitor the impacts of environmental change on these important components of marine systems (Piatt *et al.*, 2007).

My PhD provided me with a rare opportunity to utilise a comprehensive seabird diet and demographic data set, collected over a period longer than I have been alive, to test one of the most pertinent ecological questions of our time: How do populations respond to environmental change? As such, I have been able to*:*

1) *identify long-term trends in and environmental determinants of European shag Phalacrocorax aristotelis (hereafter shag) chick diet composition over a range of temporal scales, from days to decades;*
2) *quantify temporal trends in the diet of full-grown shags throughout the annual cycle, an understanding of which is absent for nearly all seabird species;*
3) *describe long-term trends in and drivers of shag productivity and phenology using one of the longest running seabird demographic datasets in existence; and*
4) *test, utilising a novel 1D methodology, trends in breeding distribution and linked reproductive consequences over two decades.*

In undertaking these analyses I have identified substantial demographic change in the Isle of May shag population, in terms of diet, phenology, productivity and fine-scale breeding distribution (Figure 25). Such rapid changes in any one of these key demographic metrics could have substantial implications for population processes and, in combination, could be catastrophic. However, my results suggest that shags in this population are adapting to pronounced environmental change (Figure 25), which may confer some resilience to predicted climate-mediated impacts in the region. In this chapter, I aim to draw together my findings, describe potential implications and highlight priorities for future research.

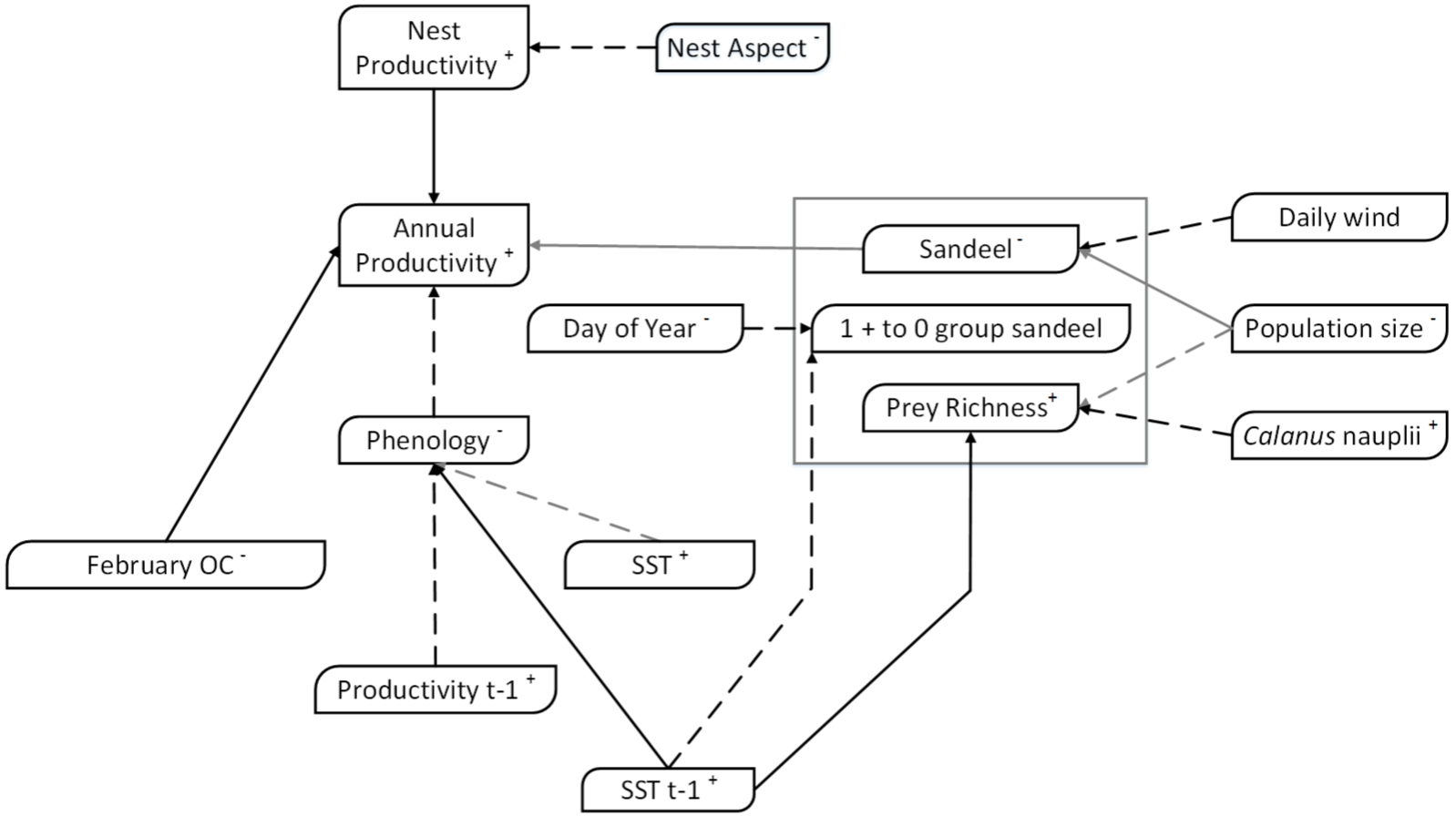

Figure 25 Schematic diagram demonstrating key links between shag demographic parameters, chick diet composition (grey box) and environmental covariates. Solid line indicates positive effect and dashed line indicates negative effect. Grey lines indicate an effect of detrending. + indicates positive trend and – indicates negative trend. Nest aspect presented as south-west relative to north east of the island. Population size displays a negative trend over the period (1985-2014) included in the diet analysis in chapter 2, not over the whole study period (1965-2014).

DIET CHANGE

By conducting the first analysis of shag diet composition on the Isle of May in over three decades, **chapter 2** redefines the feeding ecology of this population from lesser sandeel *Ammodytes marinus* (hereafter sandeel) specialists in the 1980-90s, to a diverse range of prey in recent years. This accords with wider environmental change in the North Sea associated with ocean warming, including a reduction in the abundance and size of sandeel, and a concurrent increase in prey diversity (Arnott and Ruxton, 2002; Hiddink and ter Hofstede, 2008; van Deurs *et al.*, 2009; ter Hofstede, Hiddink and Rijnsdorp, 2010). Such dietary modifications in response to changing prey populations are well reported in the literature (Montevecchi and Myers, 1996; Croxall, Reid and Prince, 1999; Montevecchi, 2007; Gaston and Elliott, 2014; Hilton *et al.*, 2015). Although the effects of wind on seabird foraging and diet composition have also been demonstrated in some species (Dunn, 1973; Elliott *et al.*, 2013), the key finding of **chapter 2** is that shag diet composition is vulnerable to both of these effects, which operate at daily and annual scales respectively. Again this links closely to the ecology of the system and shag biology, chiefly their vulnerability to wind conditions (Daunt *et al.*, 2006, 2014; Lewis *et al.*, 2015) and overall dietary flexibility (Grémillet *et al.*, 1998). One notable result was that there was no effect of the abundance of *Calanus* copepods on either sandeel relative to all prey or 1+ relative to 0 group sandeel. *Calanus finmarchicus* are a key prey species for sandeel in the North Sea, a reduction of which has been implicated in diminished sandeel recruitment (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009). However, sandeel life-history is strongly population specific, with several distinct aggregations occurring in the North Sea (Boulcott *et al.*, 2007; Rindorf *et al.*, 2016). Thus, two possible explanations for this lack of effect are that firstly, *Calanus* are of limited significance to inshore sandeel populations exploited by Isle of May shags. In an analysis of sandeel stomach content in the Firth of Forth conducted in 2012, the dominant prey were Appendicularians (Appendicularia; García *et al.* 2012). However, this study only sampled sandeel in one season, and predominantly in areas that do not overlap with the foraging distributions of Isle of May shags (Bogdanova *et al.*, 2014). Secondly, the *Calanus* measures used may not have been calculated over an appropriate spatial

and/or temporal scale to be of relevance to the sandeel populations exploited by shags. In summary, this analysis identified pronounced trends in shag chick diet and uncovered a complex suite of mechanisms that determine diet composition over a range of temporal scales.

In line with the dietary changes observed in chick diet, **chapter 3** also uncovered striking temporal trends in the diet composition of full-grown shags, again from sandeel to an increasingly diverse prey base. What is notable about this analysis is that in utilising regurgitated pellets collected throughout the annual cycle, I provide the first year round assessment of long-term dietary change in a marine top predator. Crucially, by monitoring the timing of breeding in this population, I was able to accurately assign the breeding period in each year, allowing trends in both the breeding and non-breeding period to be quantified. In contrast, the majority of seabird diet studies quantify breeding diet, in particular food destined for the brood, primarily because of the difficulty of obtaining samples in the non-breeding period (Barrett *et al.*, 2007). Altered prey availability may be particularly important during the energetically challenging winter months, when daylight is limiting and shags exist on an energetic knife-edge, with limited capacity to adjust foraging habits (Daunt *et al.*, 2014). Thus, that the diet of full-grown birds has changed throughout the annual cycle may have important implications for North Sea top predators. Shags are also considered one of the North Sea seabird species least vulnerable to changes in sandeel availability (Furness and Tasker, 2000), and so the dietary trends observed may have substantial dietary/demographic implications for other species in the region that have less capacity to switch prey.

Although the diet trends recorded in both chicks and full-grown shags displayed substantial commonality (reduction in sandeel and increase in diversity), the more marked trends in the non-breeding period identified in **chapter 3** suggest that inferring the non-breeding diet of resident top predators from data collected during breeding may provide unreliable estimates of year round resource use. However, the parallel increases in aggregate and individual-level diversity in both regurgitates and pellets suggest that, on average, the population is now exhibiting an individual generalist/population generalist, rather than an individual

specialist/population specialist structure of resource use (Bolnick *et al.*, 2003). There were also several notable differences between the diet trends recorded in **chapter 2** and **chapter 3**. First, a quadratic trend in annual Prey Richness was observed in the pellet analysis, which peaked in 2007, but not in the analysis of regurgitations. This may relate to optimal foraging theory, whereby when the availability of high quality/profitable prey is limited, adults provision chicks on more nutritionally favourable prey, while a wider range of prey are consumed by full-grown birds (Pyke, Pulliam and Charnov, 1977; Wilson, Daunt and Wanless, 2004). Second, although the increase in dietary diversification was more marked in chick diet, diet diversity in the diet of full-grown birds was consistently higher in pellets at both the sample- and annual-level. Such an effect could again arise due to parents provisioning chicks on fewer, high quality prey than consumed by themselves (Wilson, Daunt and Wanless, 2004). However, comparing the diet composition of pellets and regurgitations is problematic, since soft bodied prey are poorly represented in pellets and the number of meals/days represented is also unknown (Barrett *et al.*, 2007). These methodological differences could lead to differences in inferred diet composition even from the same individual where different techniques are used. For example, investigating Great Cormorant *Phalacrocorax carbo* diet using a combination of hard part and molecular analyses of pellets, faeces and regurgitates, led to substantial differences in inferred diet composition due to both the sample type and analysis method used (Oehm *et al.*, 2017). Irrespective of the methodological differences in sampling techniques, these results indicate substantial dietary change in both nestling and full-grown shags at this colony throughout the annual cycle over the past 3 decades. However, what is absent from these analyses, but crucial to understand more fully the link between prey availability and shag diet composition, is information on focal prey populations. Notwithstanding this, the pronounced long-term dietary changes, apparent throughout the annual cycle and driven by factors over a range of temporal scales, point towards substantial environmental change in the North Sea, which may have important implications for the demography of a suite of marine top predators in the region.

DEMOGRAPHIC CHANGE

Having investigated how the diet composition of shags on the Isle of May has changed over the past 30 years and identifying a number of important trends and drivers, **chapter 4** focused on long-term trends in two key demographic parameters, productivity and phenology. In line with **chapter 2,** this chapter incorporated environmental effects over a range of temporal scales, in addition to potential carry-over/lagged effects between different stages in the shag life cycle. To do this, two complimentary datasets were utilised. The first, chosen for temporal coverage, comprised of brood size at ringing and median ringing date, and the latter chosen for accuracy, consisted of breeding success and median laying date. These two pairs of measures accorded very closely and the results were broadly similar, so hereafter are referred to as productivity (brood size and breeding success) and phenology (ringing date and laying date) respectively (unless a specific reference is made).

Over the duration of the study, brood size increased by 16%, and ringing date advanced by ~26 days, between 1974 and 2016, with the latter a key determinant of the former (i.e. earlier seasons were more successful). Notably, conditions experienced prior to breeding and in previous seasons (February Onshore Component and previous productivity) were more important determinants of shag productivity than those occurring during breeding (weather and diet). As long-lived species, the occurrence of these lagged effects identified in **chapter 4** tie in closely with life history theory, such that previous conditions experienced may have downstream fitness consequences (Williams, 1966; Harrison *et al.*, 2011). Reproduction is costly in avian species (Daan, Deerenberg and Dijkstra, 1996; Monaghan, Nager and Houston, 1998). As such, reproduction-linked changes in individual condition can affect reproductive performance in subsequent seasons through lagged or carry-over effects (Harrison *et al.*, 2011). Previous reproduction can have negative effects on productivity between years, such that birds which are more successful breed later and less successfully the following year (Catry *et al.*, 2013; Shoji *et al.*, 2015; Fayet *et al.*, 2016). For example, in Manx shearwaters *Puffinus puffinus*, increased reproductive effort in one season led to delayed breeding and lowered reproduction the following year (Fayet *et al.*, 2016). However,

this is not always the case, as although reproduction has a negative impact on individual condition in grey-headed albatross *Thalassarche chrysostoma*, as indicated by heightened corticosterone levels, no effect on subsequent breeding was observed (Crossin *et al.*, 2017). Similarly, although successful black-headed kittiwakes *Rissa tridactyla* (hereafter kittiwake) depart the breeding grounds later than those which failed, there was no effect on subsequent breeding phenology (Bogdanova *et al.*, 2011). My analysis identified a positive effect of prior reproductive performance on population level productivity. Population breeding success provides an integrated measure of environmental conditions around the colony (Frederiksen, Mavor and Wanless, 2007). Under favourable environmental conditions in the previous season, shags may be able to produce more chicks, while on average the population may complete reproduction in a better condition. Subsequent breeding phenology may then be earlier due to enhanced mean population condition the following year. An alternative explanation is that as long-lived species, shags could defer from breeding due to a reduction in individual condition following successful reproduction (Aebischer and Wanless, 1992). Poor quality/inexperienced birds may be disproportionately affected by the costs of reproduction, with those birds that do breed of higher individual quality advancing breeding phenology in the subsequent year. Crucially, this effect of previous reproduction operated indirectly on productivity in this population, via an advancement in phenology.

Current (February/March) SST was fitted as a proxy of sandeel availability, linked to the effects of temperature on sandeel emergence prior to shag breeding (Winslade, 1974). Lagged SST was also fitted as a sandeel proxy, but in this instance the mechanism related to an effect on recruitment in the previous year (Arnott and Ruxton, 2002; Hedd *et al.*, 2006; van Deurs *et al.*, 2009). Both current and lagged SST were important determinants of breeding phenology in shags, such that breeding was earlier following warm SST in the current year and later following warmer SST in the previous year. As shags carry limited fat reserves, prey availability during the energetically challenging winter months may determine individual condition at this time of year (Grémillet *et al.*, 1999; Daunt *et al.*, 2006). Thus, the effects of current and lagged SST may be operating indirectly, relating to diet/condition linked

constraints on breeding phenology (Dawson, 2008). For example, temperature mediated increases in prey availability prior to breeding have been suggested as a mechanism driving earlier breeding in Japanese cormorant *Phalacrocorax filamentosus* in warm years (Watanuki and Ito, 2012). Alternatively, as energy expenditure is greater at lower water temperatures in shags (Enstipp *et al.*, 2007; White *et al.*, 2014), the effect of SST on phenology could also be due to a direct effect on individual condition. Shags could also use late winter SST as a cue to optimize breeding phenology in line with resource availability. For example, Cassin's auklets *Ptychoramphus aleuticus* modify breeding phenology in response to oceanic conditions, with impacts on prey availability during chick rearing (Abraham and Sydeman, 2004). However, without independent data on sandeel availability or individual data on shag physiology/energy expenditure, it was not possible to ascertain whether the effects of current/lagged SST operate as a constraint, a cue or both. In a recent review Keogan *et al.* (2018) found that globally seabird populations are not advancing their phenology in response to rising SST. Although I identified a positive effect of SST on breeding phenology in this population, this effect dropped out as a predictor of phenology following detrending, in line with this meta-analysis. Notwithstanding this, ocean warming appears to have an effect on productivity in this population, mediated via phenology.

Conditions experienced during the non-breeding period are important determinants of reproductive output in some seabirds. For example, winter body mass affects breeding propensity and success in little penguins *Eudyptula minor,* while pre-breeding diet quality alters subsequent breeding success in Cassin's auklets (Sorensen *et al.*, 2009; Salton *et al.*, 2015). In this thesis, a positive effect of February Onshore Component (poor weather conditions) on productivity was detected, possibly mediated via increased mortality and linked changes in the age/quality of breeding birds (Frederiksen *et al.*, 2008). However, no effect of breeding weather conditions on productivity were observed. Although breeding weather conditions have been shown to affect breeding success and survival in shags (Aebischer, 1993; Velando, Ortega-Ruano and Freire, 1999; Newell *et al.*, 2015) and other seabirds (Monaghan, Uttley and Burns, 1992; Schreiber, 2002; Jenouvrier, 2013; Boersma and

Rebstock, 2014), these effects are often associated with extreme weather events. Such events are generally rare, particularly on the Isle of May during summer, and so detecting an effect of weather may be difficult, since the impact of mean weather conditions may be different to those associated with extremes.

A positive effect of diet on reproduction has been observed in many seabird species, predominantly linked to increased consumption of focal prey (Monaghan *et al.*, 1989; Lewis, Wanless, *et al.*, 2001; Hedd *et al.*, 2006). However, the most common diet does not necessarily lead to higher reproductive output in marine top predators (van Donk *et al.*, 2017), while diet diversity has been linked to both increased and reduced productivity (Merrick, Chumbley and Byrd, 1997; Kowalczyk *et al.*, 2014). In this thesis, the proportion of sandeel in the diet was an important determinant of brood size (detrended), although not breeding success. Sandeel were traditionally considered one of the most profitable prey types for seabirds in the North Sea (Dunnet *et al.*, 1990; Hislop, Harris and Smith, 1991; Furness and Tasker, 2000), but recent changes in the size, calorific content and profitability of this species has been implicated in seabird breeding failures (Wanless *et al.*, 2004, 2005). In line with **chapter 2**, Wanless *et al.* (2018) recorded a decline in the size of both 1+ and 0-group sandeel consumed by Atlantic puffin *Fratercula arctica* and guillemots *Uria aalge* breeding on the Isle of May over the past three decades. Despite this reduction in size, sandeel energy density, although higher in 1+ than 0-group, was remarkably consistent across the study. This suggests that in terms of energy density at least, sandeel remain a suitable prey resource. Non-sandeel prey display similar energy densities to sandeel (Spitz *et al.*, 2010). However, differences in relative profitability due to prey behaviour, distribution or availability for example, may lead to the observed positive effect of sandeel on reproductive output.

Analyses of marine top predator demography have generally neglected within colony effects, such as microclimatic exposure and fine-scale distributional changes. In **Chapter 5,** I identified a marked distributional change around the Isle of May in mean shag nest location. However, rather than new subcolonies forming, this change was driven primarily by a reduction in the number of birds nesting on the south-west side of the island over the study, and concurrent increases in the north-east. Breeding

success was consistently higher on the north-east of the island than the south-west. This suggests that the contrasting topography on different sides of the island may be important, which may relate to more favourable breeding habitat on the east linked to nest site quality, greater exposure to prevailing weather conditions on the west, or differing foraging habitat availability on each side of the island. In **chapter 5**, I also identified an overall increase in breeding success at both the nest- and population-level, in line with **chapter 4.** However, these data comprised all nests over the entire colony, rather than only nests that were ringed (brood size at ringing) or within monitoring plots (breeding success) used in **chapter 4**, and so it is reassuring that the trends are corresponding between all three analyses. Notably however, breeding success improved more rapidly on the north-east side of the island. This could indicate that the north-east of the island has become more favourable, possibly linked to changing environmental conditions (Bonter *et al.*, 2014), or that high quality birds have been drawn to the generally more successful north-eastern subcolonies (Boulinier and Danchin, 1997). Although the relative proportion of nests on different sides on the island was not a significant determinant of population-level reproductive output, the ultimate cause of breeding success may be linked to some other factor not included in **chapter 5**, the impacts of which could vary on a nest by nest level. The relative proportion of nests on each side of the island may also be a reason why no effect of breeding season weather conditions were found on productivity in **chapter 4**, as the relative impact of meteorological conditions likely depends on the exposure of nests relative to the direction of weather, which would vary between events. Indeed poor weather may be one factor driving the distributional trends. For example, periodic severe westerly gales (Newell *et al.*, 2015), may reduce recruitment on or attraction to the exposed western shoreline. Further, as shags in this population display distinct sub-colony foraging distributions (Bogdanova et al., 2014), access to profitable foraging locations as a result of changing prey availability, as indicated by the diet trends in **chapter 2** and **3**, could be linked to the distributional change.

Although each of my analyses identified striking temporal trends, there appears to be a step change in several of the relationships around 2003-2005. This is

most apparent in the analysis of regurgitations, where the proportion of sandeel declines precipitously between 2003 and 2004, becoming more variable thereafter. A similar pattern was apparent in my analysis of pellets. There was also a pronounced distributional shift around this time, whereby the mean distance along the coastline moved from ~3000 m to ~2000m between 2003 and 2004, remaining around the latter distance thereafter. The total number of breeding events also reduced from 958 to 600 to 325, between 2003, 2004, and 2005, respectively. This suggests that some shared environmental condition may have contributed to these dietary and distributional changes, yet the mechanism remains unclear. However, two notable events occurred around this time. Firstly, 2004 was a year of reduced sandeel energy density, which was linked to reduced seabird productivity in the North Sea (Wanless *et al.*, 2004, 2005). A recent long-term analysis of community-level seabird diet energy composition on the Isle of May showed that the quality of sandeel in 2004 was lower than in any other year over the 19 years for which data were available (Wanless *et al.*, 2018). However, although the size of sandeels consumed by seabirds at this colony declined over the past three decades (in line with **Chapter 2**), sandeel energy density recovered following the extremely low values recorded in 2004 (Wanless et al., 2018). The second factor that may have contributed to this apparent step change is that a prolonged period of strong winds and heavy rain occurred in late June 2004, resulting in high shag chick mortality (Harris *et al.*, 2005). These conditions may have had contrasting effects on different sides of the colony (Newell et al., 2015). As vulnerability to poor/extreme weather varies due to sex and age in this population (Frederiksen *et al.*, 2008; Lewis *et al.*, 2015), and a decline in food quality could also have heterogeneous consequences among individuals, it is possible that these events led not only to a decline in population size, but also a change population structure, with stepped changes in subsequent behaviour, diet and demography. Thus, these effects may have led to changes in breeding distribution, due to recruitment decisions by surviving individuals. Similarly, alterations in diet may have occurred if surviving individuals had different average habitat preferences than the population prior to these events. Shags in this population are now the subject of substantial individual-level tracking, allowing the movements and life histories of single birds to be followed between years. These data may be used in

future analyses to quantify fine-scale, within colony individual movements and explore the costs/benefits associated these behaviours. Establishing the mechanisms underpinning the step change in 2003-2005 would be greatly enhanced by analysing these individual-level data. The quality of individual-level data improved markedly in 2008, and over the last 10 years an attempt is made to record all breeding events of marked individuals, which will provide excellent opportunities for individual-level analyses.

IMPLICATIONS AND FUTURE DIRECTIONS

The considerable dietary, demographic and distributional changes identified in this thesis may have a number of important implications for shags in this population. One of the most obvious likely implications of the observed dietary changes are alterations in foraging habitats. While sandeel are predominantly associated with sandy substrates, the prey consumed in recent years inhabit a range of habitats including rocky seabeds, kelp forest and soft corals (Watanuki *et al.*, 2007, 2008; Christensen-Dalsgaard *et al.*, 2017; Michelot *et al.*, 2017). This is in line with an overall reduction in the frequency of sand observed in the diet (**chapter 3**). My results suggest that climate-mediated changes in prey availability, altered shag breeding distribution and linked changes in foraging distributions, or both may be important factors. Dietary differences between the breeding and non-breeding period (**chapter 3**), may also reflect contrasting habitat use across the annual cycle (Michelot *et al.*, 2017). As habitat distributions are patchy and comparatively consistent over time in the Firth of Forth (Wanless *et al.*, 1997), dietary-mediated alterations in habitat associations will likely alter shag foraging distributions. These temporal changes in habitat association could also bring shags into conflict with previously unknown risks, such as tidal renewable developments (Bogdanova *et al.*, 2014; Daunt *et al.*, 2015; Warwick-Evans *et al.*, 2016). Individual based foraging models (Warwick-Evans *et al.*, 2018), may provide a useful assessment of these potential perturbations, particularly in light of numerous proposed renewable developments in and around the Firth of Forth.

Shags foraging in different habitats also dive at different depths, with dive depth variability greater in rocky than sandy habitats (Watanuki *et al.*, 2008). Thus, prey consumed in rocky habitats may provide a less predictable resource in terms of energy expenditure (Enstipp, Grémillet and Lorentsen, 2005). Further, males can dive more effectively due to lower mass-specific metabolic rates and greater oxygen stores (Cook *et al.* 2013), while female shags forage further away, for longer and are more strongly affected by wind (Bogdanova *et al.*, 2014; Soanes *et al.*, 2014; Lewis *et al.*, 2015). Thus, the observed diet change could have contrasting impacts between the sexes, with males potentially having a wider range of prey available and greater overall foraging flexibility.

Shags on the Isle of May display high and variable parasite loads (Burthe *et al.*, 2013). Thus, the dietary changes observed may have altered parasite burdens, with respect to both the abundance, types and diversity harboured. Such changes could have important impacts on reproductive biology by affecting parental investment or chick growth rates (Reed *et al.*, 2008; Reed *et al.*, 2012). Further, parasite load is an important determinant of flight energetics and foraging time in shags (Hicks *et al.*, 2018), which could alter the accessibility of different habitats or vulnerability to poor weather. However, longitudinal data on shag parasite load is currently relatively short (<10 years) and there is limited information regarding parasite life cycles, in particular which intermediate hosts are used amongst shag prey types. Future analyses should aim to quantify parasite loads in focal prey populations, and relate these to shag diet composition and fitness.

Changes in foraging behaviour and prey consumption may also alter foraging energetics due to differences in handling times and habitat types (Watanuki *et al.*, 2008; Udyawer *et al.*, 2017). Digestibility may also vary between prey types (Hilton, Furness and Houston, 2000), which along with variations in stomach fullness (Gommer *et al.*, 2018), could affect the relative profitability of different prey types and diet choice. For example, the diet quality of numerous seabirds was reduced when switching from their usual sandeel/clupeid prey to snake pipefish *Entelurus aequoreus* in the early-2000s, following an explosion in the abundance of the latter prey (Harris *et al.*, 2007, 2008). Diet change could also increase nutritional stress, as

indicated by elevated corticosterone levels, impairing the cognitive abilities of offspring (Kitaysky *et al.*, 2006, 2010; Will *et al.*, 2015). Thus, there are numerous intrinsic effects associated with diet change, which could operate immediately or have potential downstream consequences for individual condition, survival and recruitment.

Future analyses should aim to investigate diet at the individual level, which would make disentangling the relationships between different diet metrics, reproductive output and downstream fitness consequences more readily quantifiable. Such analyses could be undertaken utilising modern techniques such as stable isotope, fatty acid or DNA analysis (Deagle *et al.*, 2007; Bond and Jones, 2009; Owen *et al.*, 2013). Investigating individual diet would also require a more targeted sampling regime than is currently undertaken, ideally sampling the same individual multiple times over several seasons, in order to investigate individual consistency, or differences in population generalism/specialism between years (Bolnick *et al.*, 2003). However, these methods generally provide less quantitative information than analysis of hard parts from regurgitates or pellets. Quantifying the calorific content of different prey types along with provisioning rates would also be beneficial, and may provide a more mechanistic understanding of the links between diet and fitness. Combining individual level diet and tracking data could also be used to identify prey origins (Alonso *et al.*, 2018), and investigate the differences in foraging habitats and behaviours between chick- and self-feeding individuals, or between the sexes.

Increased reproductive output over the past half a century could have important implications for population age structure i.e. larger juvenile cohorts. However, recruitment appears to be limited in recent years, as although the number of chicks produced per nesting attempt has increased, the breeding population size has not. This could be caused by emigration to other colonies or high mortality in the juvenile age classes, which is already generally high (Aebischer, 1986; Frederiksen *et al.*, 2008). As shags display strong philopatry (Aebischer 1995; Barlow *et al.* 2013), the latter of these two mechanisms appears more likely and is corroborated by ringing recoveries following a string of winter mass mortality events over the past decade (unpublished data). However, shags in this population are partially migratory

(Grist *et al.*, 2017). Resident and migratory birds in this population may thus display contrasting responses to poor weather events, the impacts of which is the subject of current research. Similarly, the non-breeding dietary trends observed in **chapter 3**, may not have been apparent in those migratory birds that overwinter away from the Isle of May. Diet samples are currently being collected at overwintering sites of migrants, but are yet to be analysed. Furthermore, migration strategy affects breeding phenology and success, whereby residents breed earlier and more successfully than migrants on average (Grist *et al.*, 2017). It is possible that these effects are linked via individual decisions on where to breed on the island, and what to prey on, potentially resulting in intriguing correlations in spatial movements and diet at different scales. However, although the continued increase in reproductive output may buffer the population to the effects of poor winter weather, increases in population size may not occur if, in line with predicted increases in extreme weather events in northern latitudes (McInnes, Erwin and Bathols, 2011), the survival of both juveniles and adults is reduced in the future.

The rapid advancement in breeding phenology recorded in this population could increase trophic mismatch, particularly with species that display seasonal patterns in availability, such as sandeel (Durant *et al.*, 2005). For example, in contrast to other species on the Isle of May, shag phenology in this population displays the opposite temporal trend to sandeel size phenology (getting later), which may be indicative of trophic mismatch (Burthe *et al.*, 2012). However, given shag foraging flexibility, it is unlikely that trophic mismatch will be an important determinant of diet composition in this species, especially as shags can extract sandeel directly from the seabed (Furness and Tasker, 2000; Watanuki *et al.*, 2008). This is in contrast to other species, such as kittiwake, which are highly dependent upon coinciding their breeding with sandeel availability (Lewis, Wanless, *et al.*, 2001). Climate-mediated alterations in the availability of non-sandeel prey could also mitigate mismatch impacts. Although shags nest in all months throughout their range (Wanless and M. P. Harris, 1997), breeding phenology is likely constrained in this population by the energetically challenging winter months. However, the breeding advancement observed could allow individuals sufficient time to raise a second brood (Wanless and

M. Harris, 1997), which could further amplify the boom and bust population dynamics of this species.

The relationship between phenology and winter SST also needs to be investigated further to quantify whether this effect is operating via a constraint or a cue. Longitudinal bio-logging could be used to determine the energetic costs of foraging associated within different water temperatures, and linked phenology/reproductive consequences (Daunt *et al.*, 2014; White *et al.*, 2014). Combining independent data on prey populations with shag demography at this time of year would also be desirable, but no such data currently exist. However, if sufficient data on shag winter diet could be collected, potentially utilising alternative techniques such as DNA or stable isotope analysis or a more intensive winter sampling regime, it may be possible to link winter diet composition to environmental conditions, shag demography and carry-over effects. For example, as lagged SST may affect sandeel availability in winter, an obvious avenue for future investigation would be to test the relationship between winter sandeel consumption and lagged SST, thereby linking **chapters 2**, **3** and **4**.

The pronounced distributional change identified in **chapter 5**, suggests that shags in this population may be able to alter their fine-scale breeding distribution in response to changing environmental conditions. However, that a number of core areas remained consistent between years, presumably associated with favourable nest site characteristics and higher reproductive output, indicates that the capacity of shags to move is constrained to some extent. Attraction to these highly consistent areas may also increase breeding density, with negative impacts on reproductive output (Stokes and Boersma, 2000). As breeding success was consistently higher on the north-east side of the island, saturation of these sites could lead to further distributional trends if the population size increases in the future. The suitability of different breeding localities could also fluctuate in response to environmental conditions (Bonter *et al.*, 2014), which could themselves show trends over time. Alterations in breeding distribution could also alter vulnerability to poor weather, although this will depend on the prevailing direction relative to nesting locations (Newell *et al.*, 2015). It would be informative to relate changes in spatial distribution

to current and lagged environmental conditions, productivity, phenology and population size, in order to identify the factors driving sub colony spatial structuring.

Numerous studies have suggested that shags provide an accessible and relatively reliable indicator of prey populations, notably saithe *Pollachius virens* (Barrett, 1991; Bustnes *et al.*, 2013; Lorentsen, Anker-Nilssen and Erikstad, 2018). However, these studies have largely neglected the processes linking prey populations to shag diet composition and demography. The numerous mechanisms determining diet and demography identified in this thesis provide a substantial development in our understanding of shag foraging ecology. Thus, by combining these findings with independent data on prey populations in the Isle of May, future analyses may be able to explore the utility of shags in this population as indicators of local environmental conditions. However, given the substantial dietary and demographic flexibility observed, driven by multiple factors, it may be difficult to relate specific aspects of shag ecology/demography to wider environmental state. As such, combining multiple species breeding at this colony, including those which are more sensitive to changes in sandeel availability such as kittiwakes, may provide a more robust indicator of prey populations than shags in isolation (Durant *et al.*, 2009; Velarde, Ezcurra and Anderson, 2013; Wanless *et al.*, 2018).

Overall, the substantial dietary and demographic trends uncovered in this thesis, indicate that at both the individual- and population-level shags are responding rapidly to environmental change. However, over the study the breeding population size was highly variable (1965-2016: mean ± SD: 840 ± 450; range: 259-1916); increasing from the 1970s to the late 1990s, before plummeting in 1994, and fluctuating ever since (Figure 26). Given the dietary/demographic flexibility observed over this period, it is somewhat surprising that the population size should vary so dramatically. However, periodic mass mortality events during extreme winter weather drive population crashes on the Isle of May (Frederiksen *et al.*, 2008), the effects of which may be more catastrophic than behavioural plasticity can mitigate. However, several of my findings contribute to our understanding of the mechanisms driving the “boom and bust” population dynamics in shags. For example, the effect of wind on diet composition may be a causal factor in periodic wreck events linked

to winter storms (Aebischer and Wanless, 1992; Frederiksen *et al.*, 2008). The capacity of shags to exploit various prey types may also permit the population to increase rapidly under reduced sandeel availability or increases in non-sandeel prey. The flexible response of shags to changing environmental conditions also appears to be driving a trend in breeding distribution, with positive fitness consequences. However, shags are relatively unusual for seabirds, and the fact that these processes have been observed in this population point to pronounced environmental changes in the region. The majority of other species, particularly those that are sandeel specialists or are constrained by migration during the non-breeding period, may have limited scope to respond.

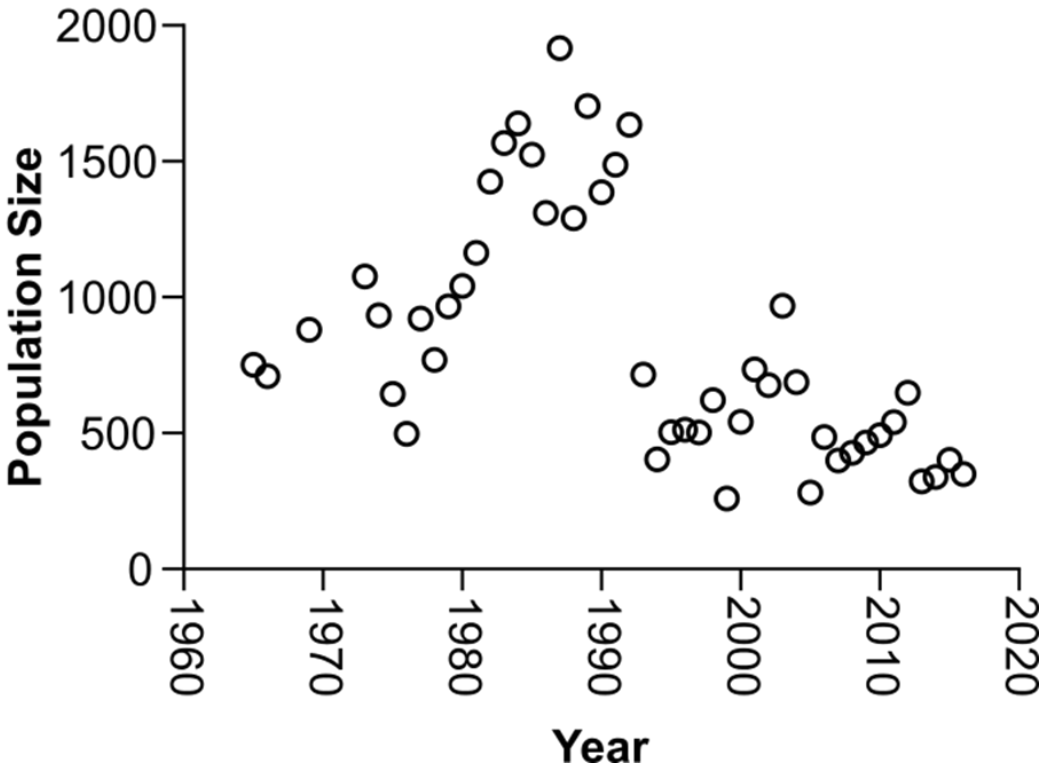

Figure 26 Interannual variation in breeding population size on the Isle of May between 1965 and 2016.

In order to develop a more mechanistic understanding of population processes at this colony, an Integrated Population Model (Besbeas *et al.*, 2002) could be constructed, incorporating the demographic change and the associated drivers of that change identified in this thesis. Utilising the considerable advancements in our understanding of shag demography may provide a more mechanistic model to be

constructed, resulting in more robust demographic predictions than were previously possible. For example, it may be possible to test under what circumstances improved productivity may buffer the population against mortality following extreme winter weather. Future work should aim to expand the analyses completed in this thesis, over a wider spatial scale and to other seabird species. This may be particularly important UK seabirds due to the substantial dietary differences, colony spatial characteristics, climate change impacts and weather conditions experienced around the UK. For example, the North Sea and Irish Sea coasts are displaying contrasting rates of warming and associated impacts on UK fish species (Heath *et al.*, 2012), which will likely be reflected in seabird dietary differences at distinct seabird colonies (Anderson *et al.*, 2014). Given the rapid population decline observed in this and other UK populations, a timely analysis would be to conduct a meta-population analysis, incorporating data from a range of UK shag colonies collected as part of the Seabird Monitoring Programme (JNCC, 2016). However, such an analysis does not need to be restricted to shags, and could incorporate multiple species (Lahoz-Monfort *et al.*, 2017) in order to identify the similarities and differences in demographic drivers throughout the UK for a guild of seabirds. Such information may further develop our understanding of community structure and responses to environmental change, highlighting priorities for future research or conservation actions.

More generally, this thesis provides a number of important developments that may be relevant to studies investigating the impacts of climate change on a wide range of species. First, **chapter 2** highlights the importance of incorporating environmental conditions calculated over a range of temporal scales into analyses of organismal responses to climatic change. Although my analysis focused on a marine top predator, these mechanisms may be equally applicable to species dependent on a wide range of resources in terrestrial, marine and freshwater habitats. Much finer resolution data (second/minutes) could also be utilised to explore the relationships between resource use and environmental conditions. **Chapter 3** demonstrates the limitations of quantifying diet or resource use over restricted periods of the annual cycle. In order to understand how species are responding to climate-mediated environmental change, it is essential to investigate resource use over the full annual

cycle and in a range of age classes. Further, although my analysis investigated year-round diet in the resident component of this population, quantifying differences in year-round resource use may be particularly important for migratory individual and species that are likely to experience substantial variability in environmental conditions and resource availability throughout the year. **Chapter 4** highlights the importance of considering lagged/carry-over effects of previous conditions in analyses of top predator demography, which may be more important determinants of population level reproductive output than those experienced during breeding. Further, as phenology was the key driver of the trends in productivity, the analysis also emphasises the importance of considering linked demographic processes in studies of population responses to climate-mediated environmental change. Finally, in **chapter 5** I show that fine-scale distributional trends are an key determinant of within-colony reproductive output, and are an important, yet often overlooked component of higher-trophic level responses to environmental change. The novel 1D framework used in **chapter 5** may also provide a relatively straightforward methodology for analysis of spatial distribution in a wide range of colonial, island breeding species, such as the intensively studied Antarctic fur seal *Arctocephalus gazelle* population on Bird Island (Boyd, 1989). However, such analyses not need be restricted to marine top predators, and could investigate fine scale distributional changes over much smaller spatial and temporal scales, and relating to a wide range of higher- and lower-trophic taxa.

CONCLUSION AND CLOSING REMARKS

This thesis has contributed to the growing body of evidence documenting rapid organismal responses to climate-mediated environmental change. In addition, these results have also redefined the feeding ecology of this population, identified pronounced demographic trends and their determinants, and, for the first time in a marine top predator, quantified long-term, fine-scale, breeding spatial dynamics. Crucially, my thesis demonstrates the importance and utility of long-term ecological monitoring, not only for understanding environmental impacts on seabirds, but in providing valuable insights into the natural world upon which we all depend. Taken together, my results suggest that shags breeding on the Isle of May display a flexible response to rapidly changing environmental conditions by adjusting their diet and breeding distribution, with demographic consequences. More generally, my results suggest potential resilience in seabirds such as shags to predicted future environmental change.

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Appendix 1

APPENDIX 1.1 FISH LENGTH/MASS EQUATIONS

Table A1 Fish otolith length/width (mm) to fish length(mm) and otolith length (mm)/otolith width (mm)/fish length (cm)to mass equations used for calculation of biomass proportions. FL = fish length (mm for column two and cm for column 5), OL = otolith length (mm), OW = otolith width (mm), M = mass (g). References: (a) Harris *et al.* (unpublished data); (b) Härkönen (1986); (c) Harris & Hislop (1978); (d) Coull *et al.* (1989); (e) Carss (1993). R2 values provided where available.

Prey	Otolith length/width (mm) to fish length (mm)	R^2	Ref	Otolith length (mm)/otolith width (mm)/fish length (cm) to fish mass	R^2	Ref
1+ group sandeel	Various [1]	-	a	$M=0.00209\ FL^{3.148}$		c
0 group sandeel	Various [1]	-	a	$M=0.00209\ FL^{3.148}$		c
Pholidae (Gunnels)	FL=11.273+ 169.26 OW	0.61	a	$M=0.0006\ FL^{3.659}$	0.86	
Gadidae (Cod fishes)	FL=-11.936+ 19.7 OL^2	0.98	b	$M=0.00854\ FL^{2.978}$ [2]		c
Callionymidae (Dragonets)	- [3]	-	-	$M=0.22\ FL^{2.5907}$ [4]		d
Cottidae (Cottids)	- [5]	-	-	$M=0.0096\ FL^{3.20}$ [6]	0.98	e
Pleuronectidae (Right-eyed Flounders)	FL=-3.81+ 47.63 OL^7	0.93	b	$M=0.0044\ FL^{3.2039}$ [8]		d
Clupeidae (Clupeids)	FL = 14.025+ 65.097 OL [9]	0.89	a	$M=0.009708\ FL^{2.855}$ [9]		c
Labridae (Wrasses)	FL = 3.05+ 3.54 OL	0.92	b	$M=3.29\ OL^{3.30}$	0.96	b
Gobiidae (Gobies)	FL = -20.41+ 87.59 OL	0.91	b	$M=0.00209\ FL^{3.148}$ [10]		c
Zoarcidae (Eelpouts)	FL = -23.65 + 179.30 OW [11]	0.83	b	$M=12.58\ OW^{4.432}$	0.83	b
Blenniidae (Blennies)	- [12]	-	-	[12]		-

[1] Used regression equations based on an annual sample of intact fish collected by mist-netting Atlantic puffins *Fratercula arctica* at this colony over the same period shag diet was sampled.
[2] Used whiting *Merlangius merlangus*.
[3] No otolith fish length equation available so used otolith length/vertebrate length relationship from sample of fish in 2012 to show that these otoliths come from small fish so set length to be 50mm.
[4] Used common dragonet *Callionymus lyra.*
[5] No otolith fish length equation available so fixed length at 100.
[6] Used sea scorpion *Taurulus bubalis.*
[7] Used plaice *Pleuronectes platessa.*
[8] Used long rough dab *Hippoglossus platessoides*.
[9] Used sprat *Sprattus sprattus.*
[10] Used sandeel.
[11] OW estimated as 25% of OL.
[12] No otoliths recovered.

Prey	Otolith length/width (mm) to fish length (mm)	R^2	Ref	Otolith length (mm)/otolith width (mm)/fish length (cm) to fish mass	R^2	Ref
Lotidae (Rocklings)	FL = 9.385+ 32.747 OL	-	a	$M=0.00209\ FL^{3.148}$ [10]		c
Syngnathidae (Pipefishes)	-[12]	-	-	-[12]	-	-

APPENDIX 1.2 COLLINEARITY IN EXPLANATORY COVARIATES

Table A2 Correlation matrix showing correlation coefficients between candidate explanatory covariates. Breeding pop. size = Breeding population size. t-1 indicates that covariates are lagged by one year.

	Day of year	**Total daily rain**	**Mean daily wind**	**SST**	**SST t-1**	***Calanus* nauplii**	***Calanus* nauplii t-1**	***C. finmarchicus***	***C. finmarchicus* t-1**	**Breeding pop. size**
Day of year										
Total daily rain	-0.05									
Mean daily wind	-0.04	-0.04								
SST	-0.32	0.07	0.02							
SST t-1	-0.05	0.03	0.13	0.36						
***Calanus* nauplii**	-0.11	-0.06	-0.03	-0.06	-0.11					
***Calanus* nauplii t-1**	-0.03	0.03	0.17	-0.19	0.07	0.08				
C. finmarchicus	0.28	-0.02	0.14	-0.10	-0.06	-0.15	0.10			
***C. finmarchicus* t-1**	0.07	0.02	-0.02	-0.45	-0.24	-0.05	-0.09	-0.15		
Breeding pop. size	0.37	0.01	0.02	-0.37	-0.42	-0.14	0.10	0.08	0.22	

APPENDIX 1.3 DETRENDING DIET MODELS

Table A3 Detrended models for each dietary component. Estimates (± SE), t-values (t) and p-values (p) reported.

Response	Fixed effect	Estimates	SE	t	p
Sandeel relative to all prey	*Mean Daily Wind Speed (ms^{-1})*	-0.06	0.03	-2.10	0.036
	Year	-14.46	3.24	-4.47	<0.001
1+ relative to 0 group sandeel	*SST t-1*	-1.99	0.73	-2.72	0.011
	Day of year	-0.09	0.01	-7.11	<0.001
	Year	-1.34	4.76	-0.28	0.780
Pholidae relative to non-sandeel prey	*SST t-1*	1.65	0.47	3.48	0.002
	C. finmarchicus abundance	-0.25	0.09	-2.69	0.013
	Year	2.54	3.76	0.68	0.507
Callionymidae relative to non-sandeel prey	*Calanus nauplii abundance*	0.05	0.02	2.92	0.008
	Calanus nauplii abundance t-1	0.05	0.02	3.12	0.005
	Year	-10.10	3.70	-2.73	0.012
Sample Prey Richness	*SST t-1*	0.98	0.27	3.60	0.001
	Calanus nauplii abundance	-0.03	0.01	-2.83	0.009
	Year	10.32	1.80	5.72	<0.000

APPENDIX 1.4 DIETARY TRENDS

Table A4 Modelled response variables and fixed effects included in trends analysis of diet proportions and sample-level Prey Richness. Estimates (±SE), t-values (t) and as backwards-stepwise deletion was used, p-values (p) are reported.

Response	Trend	Fixed effect	Est	SE	t	p
Sandeel relative to non-sandeel prey	Linear	*Year*	-14.49	3.22	-4.50	<0.001
	Linear & Quadratic	*Year*	-14.30	3.27	-4.37	<0.001
		$Year^2$	29.88	41.25	0.72	0.475
1+ group relative to 0 group sandeel	Linear	*Year*	4.65	5.42	0.86	0.398
	Linear & Quadratic	*Year*	3.36	5.67	0.59	0.558
		$Year^2$	-46.09	67.73	-0.68	0.502
Pholidae relative to other non-sandeel prey	Linear	*Year*	5.48	4.17	1.31	0.202
	Linear & Quadratic	*Year*	9.10	5.61	1.62	0.119
		$Year^2$	-79.72	62.71	-1.27	0.216
Callionymidae relative to other non-sandeel prey	Linear	*Year*	-13.91	4.84	-2.87	0.008
	Linear & Quadratic	*Year*	-13.54	4.95	-2.74	0.012
		$Year^2$	59.59	62.55	0.95	0.351
Gadidae relative to other non-sandeel prey	Linear	*Year*	-0.10	4.69	-0.02	0.984
	Linear & Quadratic	*Year*	1.00	5.25	0.19	0.850
		$Year^2$	-58.63	66.22	-0.89	0.385
Sample-level Prey Richness	Linear	*Year*	12.09	2.37	5.09	<0.001
	Linear & Quadratic	*Year*	12.25	2.45	5.00	<0.001
		$Year^2$	-27.21	30.22	-0.90	0.376

Appendix 2

APPENDIX 2.1 MONTHLY PELLET SAMPLE SIZES

Table A5 Sample size of pellets in each month between 1985-86 and 2014-15. Bold values indicate breeding period in each year. The non-breeding period in each year starts in the month after the breeding period and ends in the month preceding the commencement of the breeding period in the following calendar year.

Year	Month												
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Total**
1985	-	-	-	-	**0**	**0**	**0**	**0**	0	53	0	0	53
1987	0	0	0	**0**	**0**	**0**	**0**	0	0	30	0	0	30
1988	0	0	40	39	**31**	**10**	**30**	**24**	0	0	29	0	203
1989	0	0	38	27	**65**	**83**	**67**	**40**	42	157	30	0	549
1990	29	36	40	93	111	**80**	**80**	**99**	**80**	75	0	0	723
1991	0	0	69	119	102	**70**	**91**	**55**	**60**	61	0	0	627
1992	0	0	80	93	**65**	**56**	**110**	**78**	19	30	0	0	531
1993	0	41	43	40	76	**79**	**40**	**0**	**0**	0	0	0	319
1994	0	0	9	29	**28**	**43**	**31**	**21**	0	0	0	0	161
1998	0	0	0	0	**0**	**0**	**49**	**0**	0	0	0	0	49
1999	0	0	0	0	**0**	**153**	**189**	**0**	0	0	0	0	342
2003	0	0	0	**0**	**0**	**10**	**72**	20	0	0	0	0	102
2004	0	0	0	0	**26**	**83**	**97**	**16**	0	0	0	0	222
2005	0	0	12	101	**104**	**54**	**54**	**22**	0	9	0	27	383
2006	23	17	38	51	**91**	**83**	**24**	**27**	0	28	0	0	382
2007	15	0	29	22	**8**	**29**	**59**	**16**	0	0	0	0	178
2008	0	0	0	25	**0**	**21**	**10**	**0**	0	0	0	0	56
2009	0	0	0	**24**	**30**	**29**	**19**	0	10	0	0	0	112
2010	18	0	26	**0**	**8**	**6**	**37**	15	31	0	0	18	159
2011	0	18	4	**0**	**5**	**17**	**4**	63	35	0	16	11	173
2012	28	23	33	**0**	**1**	**36**	**41**	18	52	30	17	16	295
2013	42	11	0	0	**0**	**9**	**19**	**7**	0	15	0	33	136
2014	20	28	0	**0**	**1**	**20**	**14**	20	0	0	0	0	103
2015	0	0	0	**-**	**-**	**-**	**-**	-	-	-	-	-	0

APPENDIX 2.2 ANNUAL BREEDING AND NON-BREEDING PERIOD DURATIONS

Table A6 Start month, end month and length (in months) of breeding and non-breeding periods in each study year, together with the total number of months contributing to each study year.

Year	Breeding			Non-breeding			Total
	Start	End	Length	Start	End	Length	
1985-86	May	August	4	Sept	March	7	11
1987-88	April	July	4	August	March	8	12
1988-89	April	July	4	Sept	April	8	12
1989-90	May	August	4	September	April	8	13
1990-91	June	September	4	October	May	8	12
1991-92	June	September	4	October	April	7	11
1992-93	May	August	4	September	May	9	13
1993-94	June	September	4	October	April	7	11
1994-95	May	August	4	September	March	7	12
1998-99	May	August	4	September	April	8	12
1999-00	May	August	4	September	April	8	12
2003-04	April	July	4	August	April	9	13
2004-05	May	August	4	September	April	8	12
2005-06	May	August	4	September	April	8	12
2006-07	May	August	4	September	April	8	12
2007-08	May	August	4	September	April	8	12
2008-09	May	August	4	September	April	8	12
2009-10	April	July	4	August	March	8	12
2010-11	April	July	4	August	March	8	12
2011-12	April	July	4	August	March	8	12
2012-13	April	July	4	August	March	8	12
2013-14	May	August	4	September	April	8	12
2014-15	April	July	4	August	March	8	12

APPENDIX 2.3 FULL MODEL SELECTION TABLES FOR FREQUENCY OF OCCURANCE

Table A7 Full model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*)on presence of each prey type. Table shows model rank compared to other models, model structure, number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ω_i). Top models are shown in **bold**.

Response	Rank	Model	k	Δ AICc	ω_i
Sandeel	**1**	***Year + Period + Year*Period***	**5**	**0.00**	**1.00**
	2	*Year*	3	15.38	<0.01
	3	*Year + Period*	4	16.76	<0.01
	4	*i*	2	25.75	<0.01
	5	*Period*	3	27.12	<0.01
Gadidae	**1**	***Year***	**3**	**0.00**	**0.43**
	2	*Year + Period + Year*Period*	5	0.12	0.41
	3	*Year + Period*	4	1.95	0.16
	4	*i*	2	17.44	<0.01
	5	*Period*	3	18.9	<0.01
Gobiidae	**1**	***Year + Period + Year*Period***	**5**	**0.00**	**0.78**
	2	*Year + Period*	4	2.57	0.22
	3	*Year*	3	12.35	<0.01
	4	*Period*	3	12.63	<0.01
	5	*i*	2	22.66	<0.01
Pleuronectidae	**1**	***Year + Period + Year*Period***	**5**	**0.00**	**0.98**
	2	*Year + Period*	4	8.96	0.01
	3	*Year*	3	10.34	0.01
	4	*Period*	3	11.82	<0.01
	5	*i*	2	13.37	<0.01
Cottidae	**1**	***Year***	**3**	**0.00**	**0.64**
	2	*Year + Period*	4	2.00	0.24
	3	*Year + Period + Year*Period*	5	3.30	0.12
	4	*i*	2	19.1	<0.01
	5	*Period*	3	21.07	<0.01
Sand	**1**	***Year + Period + Year*Period***	**5**	**0.00**	**1.00**
	2	*Year + Period*	4	13.44	<0.01
	3	*Period*	3	23.41	<0.01
	4	*Year*	3	93.67	<0.01
	5	*i*	2	102.36	<0.01

APPENDIX 2.4 FULL MODEL SELECTION TABLES FOR NUMERICAL ABUNDANCE

Table A8 Full model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on numerical abundance of sandeel (relative to all otoliths) and Gadidae (relative to all non-sandeel otoliths). Table shows model rank compared to other models, model structure, number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ωi). Top models are shown in **bold**.

Response	Rank	Model	k	Δ AICc	ω_i
Sandeel	**1**	***Year***	**3**	**0.00**	**0.65**
	2	*Year + Period*	4	1.89	0.25
	3	*Year + Period + Year*Period*	5	3.89	0.09
	4	*i*	2	25.24	<0.01
	5	*Period*	3	26.5	<0.01
Gadidae	**1**	***Year + Period***	**4**	**0.00**	**0.92**
	2	*Year*	3	5.21	0.07
	3	*Year + Period + Year*Period*	5	8.84	0.01
	4	*i*	2	79.63	<0.01
	5	*Period*	3	81.67	<0.01

APPENDIX 2.5 FULL MODEL SELECTION TABLES FOR PREY RICHNESS

Table A9 Full model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on sample-level Prey Richness, and linear and quadratic trends in annual Prey Richness. Annual Prey Richness is fitted with a log(number of pellets year^{-1}) offset. Table shows model rank compared to other models, model structure, number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ωi). Top models are shown in **bold**. Models with similar levels of support indicated with †.

Response	Rank	Model	k	Δ AICc	ω_i
Sample Prey Richness	**1**	***Year + Period + Year*Period***	**5**	**0.00**	**1.00**
	2	*Year + Period*	4	23.84	<0.01
	3	*Year*	3	32.04	<0.01
	4	*Period*	3	45.01	<0.01
	5	*i*	2	54.95	<0.01
Annual Prey Richness	**1**	***Year + Year^2***	**5**	**0.00**	**0.66**
	2†	*Year*	4	1.33	0.34
	3	*i*	3	12.14	<0.01

Appendix 3

APPENDIX 3.1 CORRELATION BETWEEN BROOD SIZE AND BREEDING SUCCESS AND RINGING DATE AND LAYING DATE

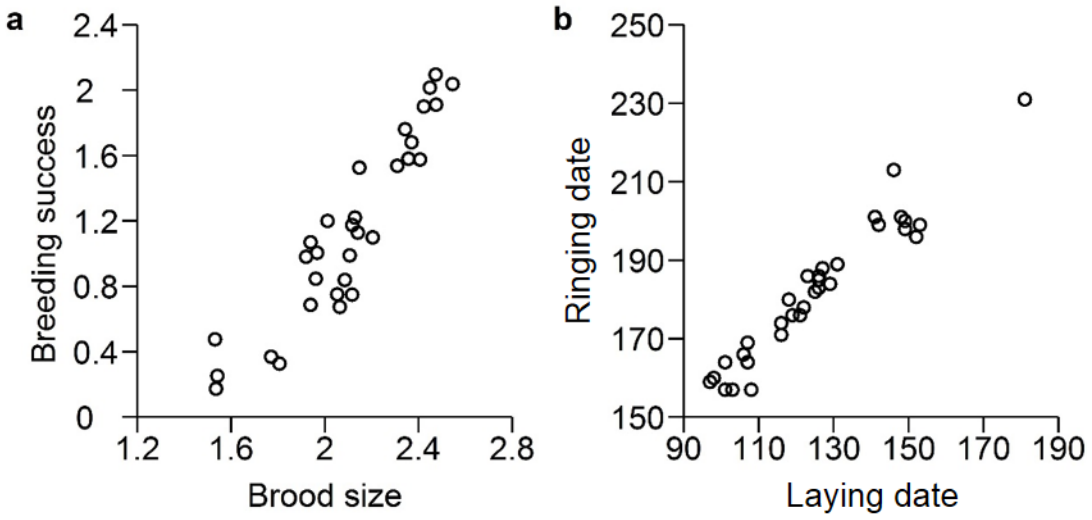

Figure A1 Correlation between a) brood size and breeding success; and b) laying date and ringing date between 1986-2016.

APPENDIX 3.2 SUPPLEMENTARY ANALYSIS OF BREEDING SUCCESS AND LAYING DATE

INTRODUCTION

To complement my main analysis of brood size and ringing date I also completed a supplementary analysis of breeding success and laying date. These data were collected over a more recent run of years (1986-2016), through which the population has been monitored more intensively.

METHODS

DEMOGRAPHIC RESPONSE VARIABLES

The study was conducted on the Isle of May National Nature Reserve, southeast Scotland (56°11'N, 02°33'W). Annually between 1986 and 2016, breeding success (number of chicks fledged; n = 3967; mean ± SD: 127.98 ± 72.92 year^{-1}; range: 14-317) and breeding phenology (laying date) were recorded from a sample of nests (n = 3659; mean: 118.03 ± 63.77 year^{-1}; range: 42-288) in 9-14 monitoring plots distributed throughout the island (Newell *et al.*, 2015), using standardised methods (Walsh *et al.* 1995). From these, I calculated annual mean breeding success (hereafter breeding success) and median laying date (hereafter laying date).

EXPLANATORY VARIABLES

To test the relative importance of direct and indirect environmental change on breeding success, and whether these effects operate immediately, are delayed, or are mediated via laying date, I selected the following suite of explanatory variables. Variables were collated between 1987 and 2016 (1986 for lagged variables) as this was the first year over which all explanatory variables was available.

EXPLANATORY VARIABLES

To test the relative importance of direct and indirect environmental change on breeding success, and whether these effects operate immediately, are delayed, or are mediated via laying date, I selected the following suite of explanatory variables. Variables were collated between 1986 and 2016, to match the duration of the

response variables. Thus, trends analyses of breeding success and laying date was undertaken between 1986 and 2016. Covariate analysis covariate analyses of breeding success and laying date ran between 1987 (as lagged variables were only available from this date) and 2016.

IMMEDIATE EFFECTS

PROXIES OF SANDEEL AVAILABILITY

Availability of principal prey is a key determinant of demography in many seabirds (Monaghan *et al.*, 1989). Although the lagged, larval Sandeel Biomass Index has previously been shown as an important determinant of shag breeding productivity in this population (Frederiksen, Furness and Wanless, 2007), these data were unavailable for the majority of the study period. Thus, I utilised three proxies of sandeel availability in my analysis in order to determine whether changes in diet could be linked to brood size: a) Sea Surface Temperature (hereafter SST); b) SST in the previous year; and c) diet.

Sandeel abundance is determined by SST, via indirect bottom-up effects mechanisms (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009; Rindorf *et al.*, 2016). Monthly SST data were obtained from the German 'Bundesamt fur Seeschiffart und Hydrographie' (http://www.bsh.de) between 1973 and 2016, following Frederiksen *et al.* (2004). Spring SST (average of mean February and March; i.e. peak months of sandeel hatching; Macer 1966, Wright & Bailey 1996) were extracted for an inshore area surrounding the Isle of May (bounded by c. 56°0'N and 56°4'N, and 2°7'W and 2°3'W), encompassing the summer foraging range of this population (Bogdanova *et al.*, 2014). 1+ sandeel form a substantial part of the diet in this population, the proportion of which is determined by SST in the previous year (Howells *et al.*, 2017). Thus, I also included SST lagged by one year. Although lagged, the mechanism through which I believe this effect to be operating is via impacts on sandeel availability in the current year and so I consider this effect to be a proxy of immediate conditions. I also tested the effect of the proportion of sandeel in chick diet (hereafter proportion of sandeel), following methods in (Howells *et al.*, 2017).

Population size

Changes in population size at this colony may impact brood size via density dependent effects, which have been shown to affect shag reproductive output (Potts, Coulson and Deans, 1980; Aebischer, 1985). Thus, to examine the effects of density dependence on breeding success and laying date I estimated the number of breeding pairs using standardised protocols (apparently occupied nests; see Walsh *et al.* 1995), hereafter referred to as population size.

Prevailing weather conditions

Shag foraging performance is strongly affected by wind in this population (Daunt *et al.*, 2006, 2014; Lewis *et al.*, 2015; Kogure *et al.*, 2016), which may alter the capacity of parents to provision the brood. Furthermore, young chicks are vulnerable to exposure to strong winds and heavy rain (Snow 1960, Aebischer 1985, Daunt *et al.* 1999, Velando *et al.* 1999). To test the effects of breeding season weather, hourly wind and rain data were obtained from Leuchars weather station (56°23'N, 2°52'W; c.28 km from the study site; http:// badc.nerc.ac.uk), between 1974-2016. Following Frederiksen *et al.* (2008), I calculated mean daily wind speed (knots) * sin(mean daily wind direction), and set it to 0 if the wind direction was westerly i.e. between 180° and 360°. I used the first 28 days after median hatching date (hereafter early chick-rearing period) to encompass the period of chick vulnerability, and the same duration as Frederiksen *et al.* (2008). To calculate median hatch date from median laying date I added the average incubation duration, 36 days (Potts, Coulson and Deans, 1980). To calculate the first month after hatching I then added 27 days to each of the predicted hatching dates and calculated summed breeding season Onshore Component (hereafter breeding Onshore Component) and Total Precipitation (hereafter breeding Total Precipitation) during the early chick ringing period.

Delayed effects

Previous reproduction and phenology

Long-lived species, such as shags, must balance the trade-off between current reproductive investment and lifetime fecundity (Williams, 1966). Costs associated with previous reproduction, may alter individual condition and, in turn, breeding

phenology and breeding productivity in the current year (Inger *et al.*, 2010; Catry *et al.*, 2013). Breeding productivity likely represents an integrated measure of environmental conditions (Frederiksen, Mavor and Wanless, 2007), so any relationship between past and current reproductive output may equate to a lagged effects of environmental conditions in the previous year. Therefore, I breeding success and laying date in the previous year in the analysis to test for any downstream effects of costs associated with/conditions experienced during previous reproduction.

FEBRUARY WEATHER

Winter weather conditions, in particular onshore (i.e. easterly) winds and precipitation during February, have previously been shown to affect breeding phenology in this population (Aebischer, 1986; Aebischer and Wanless, 1992; Daunt *et al.*, 2006, 2014). Survival probability is also lower when winter weather is poor (Frederiksen *et al.*, 2008), and surviving birds could experience reduced individual condition with knock-on effects on productivity. Thus, daily Onshore Component values were summed over February in each year to calculate an annual February Onshore Component in line with Frederiksen *et al.* 2008. February Total Precipitation comprised summed hourly precipitation over February in each year. Both variables had the same duration and method of processing the data as the breeding weather variables.

STATISTICAL MODELLING

RATIONALE

Given the prediction that breeding phenology influences breeding productivity in shags, elucidating the drivers of breeding success also requires an understanding of which factors determine laying date. Thus, I structured my analysis in two steps. First, I tested the explanatory covariates, including laying date, of trends and variability in breeding success. Then, in a second step, I tested the explanatory covariates of trends and variability in laying date, including only those variables that preceded laying date in the year of interest. This structured analysis allowed me to determine

whether the explanatory covariates operate directly on breeding success or mediated via impacts on laying date. Trends in breeding success and laying date are presented in the main analysis (Table 12; Figure 15).

DEMOGRAPHIC VARIABLES

All data manipulation and statistical modelling was conducted using the R programming language (R Development Core Team 2015). To avoid predicted values being higher than the maximum number of chicks fledged in this population (4; Harris *et al.* 1994) or below 0, I adopted a binomial modelling approach for breeding success (Cook *et al.*, 2014; Carroll *et al.*, 2015). Thus, breeding success was modelled as the total number of chicks fledged year^{-1}/ (number of nests monitored* 4).

COVARIATE MODELS

To test the determinants of breeding success I fitted Generalised Linear Mixed Models (hereafter GLMMs) with a binomial error and logit-link function using *glmer* function, in the *lme4* package (Bates *et al.* 2015). To account for overdispersion, year was included as a sample-level categorical random effect. I fitted a global GLMM containing each of my explanatory variables: SST, SST t-1, proportion of sandeel, population size, breeding Onshore Component, breeding Total Precipitation, laying date, laying date t-1, breeding success t-1, February Onshore Component, and February Total Precipitation. To test the determinants of laying date, I fitted a global Linear Model (hereafter LMs) including the following variables: SST, SST t-1, breeding population size, laying date t-1, brood size t-1, February Onshore Component, and February Total Precipitation. It was not necessary to include an AR term in models of breeding success and laying date, as breeding success t-1 and laying date t-1, were included as a fixed effects in the model selection process.

Model comparison was conducted using Akaike's Information Criterion corrected for small sample size (AICc). Models within 2 AICc of the best supported model (lowest AICc) were considered to have strong support, unless they contained an additional parameter, in which case they were regarded as uninformative and not considered (Burnham and Anderson, 2002; Arnold, 2010). For all models, the distribution of residuals indicated no violation of normality or homoscedasticity assumptions.

As sufficient temporal coverage of predictor variables did not commence until 1987, covariate models of breeding success and laying date were restricted to 1987-2016. I had no biological *a priori* reason to test for interaction terms and thus my analysis considered main effects only. All explanatory variables were scaled and centred to make effect sizes comparable (mean = 0; SD = 0) and to avoid model convergence issues.

A requirement of the linear modelling approach is that covariates within the same models are not collinear. Thus, to test for collinearity between covariates, I calculated Pearson's Correlation Coefficients between each of my predictor variables (Table A10). Where substantial collinearity was identified ($r > 0.6$), those variables were not permitted together in the same candidate model. This included: SST and February OC ($r = -0.61$), breeding success t-1 and laying date ($r= -0.62$), and breeding success t-1 and laying date t-1 ($r= -0.71$).

Table A10 Pearson's correlation coefficients between each of the explanatory covariates used in the model selection process of breeding success and laying date between 1986 and 2016. OC = Onshore Component. TP = Total Precipitation. Highly correlated variables (R > 0.60) are indicated in bold.

	Breeding success t-1	Laying date t-1	February OC	February TP	Breeding OC	Breeding TP	SST	SST t-1	Proportion of sandeel	Population size	Laying date
Breeding success t-1											
Laying date t-1	**-0.71**										
February OC	-0.25	0.49									
February TP	0.00	0.31	0.23								
Breeding OC	0.10	0.09	0.09	0.15							
Breeding TP	0.16	-0.15	-0.26	0.25	0.25						
SST	0.22	-0.33	**-0.61**	-0.08	0.04	0.24					
SST t-1	0.16	-0.28	-0.13	-0.21	-0.17	-0.26	0.30				
Prop. of sandeel	-0.15	0.21	0.11	0.28	-0.10	-0.04	-0.18	-0.44			
Population size	-0.21	0.32	0.01	-0.08	0.12	-0.01	-0.15	-0.36	0.54		
Laying date	**-0.62**	0.34	0.18	-0.15	-0.18	-0.33	-0.27	0.23	0.05	0.20	

When trends are present in both response and explanatory variables spurious results may occur (Grosbois *et al.*, 2008). Thus, as I identified temporal trends in some of the covariates, I undertook a supplementary detrending analysis, in which a linear, fixed effect of year was fitted in all explanatory models of breeding success and laying date during the modelling process. In doing so, I removed any temporal trends form the response variables. Model support was compared between the non-detrended and detrended models. Where differences occurred this suggests that support identified in the non-detrended analysis may be due to correlation with a third variable that is also displaying a temporal trend, and should be treated with caution.

As a Poisson error structure could be a valid distribution for breeding success I undertook a further supplementary analysis, in which I fitted GLMMs with a Poisson error distribution and a log(number of nests) offset. Results were comparable between the two modelling approaches and thus I consider the use of binomial analyses appropriate.

RESULTS

EXPLANATORY COVARIATES OF BREEDING SUCCESS

The best supported model for breeding success contained a negative effect of laying date and a positive effect of February Onshore Component (Table A11; extended model selection table presented in Table A13; Figure A2). Breeding success was reduced when the laying date was later, from 1.98 chicks fledged $nest^{-1}$ at 97 days (~6th April) to 0.24 chicks fledged $nest^{-1}$ at 181 days (~29th June; Figure A2a). Breeding success increased from 0.89 chicks fledged $nest^{-1}$ at a February Onshore Component of 0 to 1.85 chicks fledged $nest^{-1}$ at a February Onshore Component of 231 (Figure A2b). Two models were considered to have similar levels of support: a model containing a negative effect of laying date only; and a model containing a positive effect of laying date lagged by a year and a negative effect of laying date in the current year (Table A11). Both models contained an effect of laying date, providing strong support for this variable. Although laying date in the current year was retained in the best supported model following detrending, February Onshore Component was drooped, and top model also contained a positive effect of laying date in the previous year (Table A14). In the analysis conducted with a Poisson error structure, the best supported model also contained an effect of laying date and February Onshore Component only (Table A15). There here was limited evidence that current or lagged SST, the proportion of sandeel in the diet, breeding season weather conditions, population size, February total precipitation, or breeding success/laying date in the previous year, were important determinants of breeding success.

Table A11 Model selection table and effect sizes for binomial GLMMs of breeding success modelled between 1987-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For each fixed effect I report an estimate (± SE) and z-value. The number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 2 AICc of the top model. The best supported model is shown in **bold**, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	Estimate	SE	z	k	ΔAICc	ω_i
1	***Laying date + February OC***				**5**	**0.00**	**0.09**
	Laying date	**-0.49**	**0.07**	**-6.79**			
	February OC	**0.15**	**0.07**	**2.11**			
2	*Laying date + SST t-1 + February OC*				6	1.40	0.04
	Laying date	-0.52	0.07	-7.04			
	SST t-1	0.09	0.07	1.25			
	February OC	0.15	0.07	2.24			
3†	*Laying date*				4	1.53	0.04
	Laying date	-0.48	0.08	-6.21			

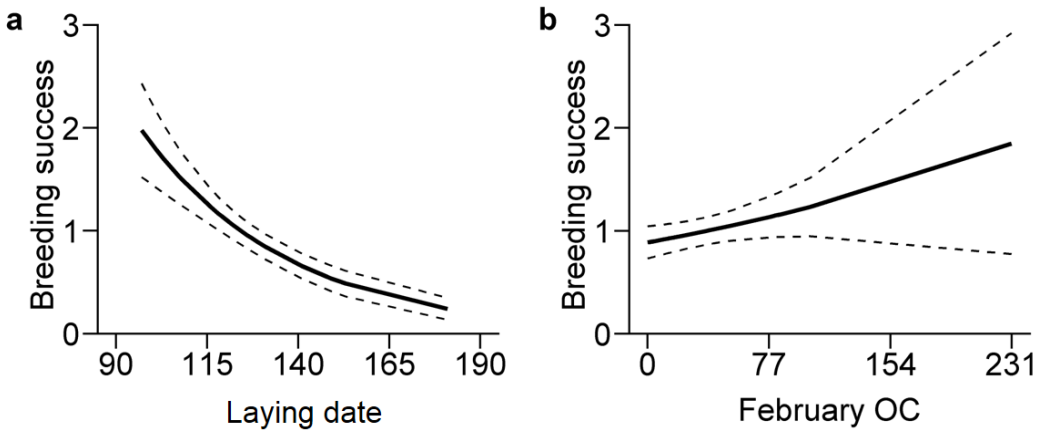

Figure A2 Fitted lines (±95 % CI) for the relationship between breeding success and a) laying date and b) February Onshore Component. Values are displayed over the range for which data were included in the model. Predictions were made using binomial GLMMs, setting additional fixed effects at the mean value. Predicted lines are shown as solid lines and confidence intervals as dashed lines.

EXPLANATORY COVARIATES OF LAYING DATE

The best supported model for laying date contained a negative effect of SST in the current year, a positive effect of SST in the previous year and a negative effect of breeding success in the previous year (Table A12; extended model selection table presented in Table A16). Warmer SST in the current year was associated with an advancement in laying, from 116 days (~26th April) at 6.78 °C to 137 days (~26th April) at 4.45 °C (Figure A3a). Laying date was earlier following cooler SST in the previous year, from 106 days (~16th April) at 4.45 °C to 138 days (~18th May) at 6.78 °C (Figure A3b). Laying date was earlier following high breeding success in the previous year, from 145 days (~25th May) at 0.18 chicks nest^{-1} to 104 days (~14th April) at a 2.04 chicks nest^{-1} (Figure A3c). Two other models received similar levels of support, including a model containing an effect of SST and breeding success in the previous year, and a model containing and SST in the previous year, population size and breeding success in the previous year. In the detrending analysis, the effect of SST in the current year was dropped from the best supported model, which contained an effect of breeding success and SST in the previous year, and year, and outperformed all others in the detrended model set (Table A17). There was no evidence of an effect breeding or February weather conditions or laying date in the previous year, on laying date.

Table A12 Model selection table and effect sizes for Linear Models of laying date modelled between 1987-2016. For each fixed effect within a model, I report an estimate (± SE) and t-value. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Only models with relatively strong support (ΔAICc <2) presented. The best supported model is shown in **bold**, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	Est	SE	t	k	ΔAICc	ω_i
1	***SST + SST t-1 + Breeding success t-1***				**5**	**0**	**0.23**
	SST	**-5.06**	**2.71**	**-1.86**			
	SST t-1	**8.04**	**2.68**	**3**			
	Breeding success t-1	**-12.34**	**2.62**	**-4.71**			
2	*SST + SST t-1 + Population size + Breeding success t-1*				6	0.51	0.18
	SST	-5.02	2.65	-1.89			
	SST t-1	9.38	2.76	3.39			
	Population size	4.06	2.7	1.51			
	Breeding success t-1	-11.7	2.59	-4.51			
3†	*SST t-1 + Breeding success t-1*				4	0.89	0.15
	SST t-1	6.64	2.68	2.48			
	Breeding success t-1	-13.25	2.68	-4.94			
4†	*SST t-1 + Population size + Breeding success t-1*				5	1.4	0.11
	SST t-1	8.01	2.79	2.87			
	Population size	4.11	2.82	1.46			
	Breeding success t-1	-12.59	2.67	-4.72			

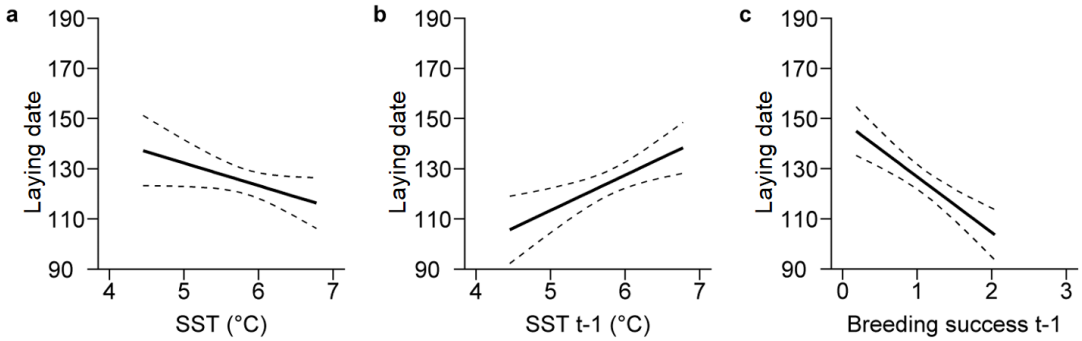

Figure A3 Fitted lines (±95 % CI) for the relationship between laying date (day of year) and a) SST in the current year; b) SST in the previous year; and c) breeding success in the previous year. t-1 indicates covariates lagged by one year. Values are displayed over the range for which data were included in the model. Predictions were made using LMs, setting additional fixed effects at the mean value.

Table A13 Extended model selection table for binomial Generalised Linear Mixed Effect Models fitted for breeding success, modelled between 1987-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparison the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. The best supported model is shown in **bold**, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	k	ΔAICc	ω_i
1	***Laying date + February OC***	**4**	**0.00**	**0.09**
2	*Laying date + SST t-1 + February OC*	5	1.40	0.04
3†	*Laying date*	3	1.53	0.04
4	*Laying date + Breeding TP + February OC*	5	2.05	0.03
5	*Laying date + SST t-1 + Laying date t-1*	5	2.17	0.03
6	*Laying date + Laying date t-1*	4	2.30	0.03
7	*Laying date + February OC + Laying date t-1*	5	2.57	0.02
8	*Laying date + February OC + February TP*	5	2.58	0.02
9	*Laying date + Population size + February OC*	5	2.88	0.02
10	*Laying date + Proportion of sandeel + February OC*	5	2.90	0.02
11	*Laying date + Breeding OC + February OC*	5	2.90	0.02
12	*Laying date + Breeding TP*	4	3.04	0.02
13	*Laying date + SST t-1 + February OC + Laying date t-1*	6	3.13	0.02
14	*Laying date + SST t-1*	4	3.18	0.02
15	*Laying date + SST*	4	3.95	0.01
16	*Laying date + Breeding TP + Laying date t-1*	5	3.96	0.01
17	*Laying date + SST t-1 + Population size + February OC*	6	4.01	0.01
18	*Laying date + Breeding OC*	4	4.07	0.01
19	*Laying date + February TP*	4	4.11	0.01
20	*Laying date + Population size*	4	4.18	0.01
21	*Laying date + Proportion of sandeel + SST t-1 + February OC*	6	4.19	0.01
22	*Laying date + SST t-1 + Breeding TP + February OC*	6	4.20	0.01
23	*Laying date + Proportion of sandeel*	4	4.20	0.01
24	*Laying date + SST t-1 + February OC + February TP*	6	4.47	0.01
25	*Laying date + SST t-1 + Breeding OC + February OC*	6	4.51	0.01
26	*Laying date + SST + SST t-1 + Laying date t-1*	6	4.76	0.01
27	*Laying date + Breeding TP + February OC + Laying date t-1*	6	4.80	0.01
28	*Laying date + Population size + Laying date t-1*	5	4.89	0.01
29	*Laying date + SST t-1 + Breeding TP + Laying date t-1*	6	4.93	0.01
30	*Laying date + Proportion of sandeel + SST t-1 + Laying date t-1*	6	4.98	0.01
31	*Laying date + Breeding TP + February OC + February TP*	6	5.08	0.01
32	*Laying date + February TP + Laying date t-1*	5	5.12	0.01
33	*Laying date + Breeding TP + Population size + February OC*	6	5.14	0.01

Rank	Model	k	ΔAICc	ω_i
34	*Laying date + February OC + February TP + Laying date t-1*	6	5.15	0.01
35	*Laying date + Proportion of sandeel + Laying date t-1*	5	5.15	0.01
36	*Laying date + SST + Laying date t-1*	5	5.16	0.01
37	*Laying date + Breeding TP + Breeding OC + February OC*	6	5.16	0.01
38	*Laying date + Breeding OC + Laying date t-1*	5	5.18	0.01
39	*Laying date + SST t-1 + Breeding OC + Laying date t-1*	6	5.18	0.01
40	*Laying date + Proportion of sandeel + Breeding TP + February OC*	6	5.20	0.01
41	*Laying date + SST + SST t-1*	5	5.25	0.01
42	*Laying date + SST t-1 + February TP + Laying date t-1*	6	5.31	0.01
43	*Laying date + SST t-1 + Population size + Laying date t-1*	6	5.32	0.01
44	*Laying date + SST t-1 + Breeding TP*	5	5.38	0.01
45	*Laying date + Breeding TP + Breeding OC*	5	5.58	0.01
46	*Laying date + Breeding TP + February TP*	5	5.67	0.01
47	*Laying date + Proportion of sandeel + February OC + Laying date t-1*	6	5.70	0.01
48	*Laying date + Proportion of sandeel + February OC + February TP*	6	5.70	0.01
49	*Laying date + Population size + February OC + February TP*	6	5.71	0.01
50	*Laying date + Population size + February OC + Laying date t-1*	6	5.71	0.01
51	*Laying date + Breeding OC + February OC + Laying date t-1*	6	5.72	0.01
52	*Laying date + SST + Breeding TP*	5	5.73	0.01
53	*Laying date + Proportion of sandeel + SST t-1*	5	5.73	0.01
54	*Laying date + Breeding OC + February OC + February TP*	6	5.74	0.01
55	*Laying date + SST t-1 + February TP*	5	5.74	0.01
56	*Laying date + SST t-1 + Breeding OC*	5	5.77	0.01
57	*Laying date + Proportion of sandeel + Breeding TP*	5	5.93	<0.01
58	*Laying date + Breeding TP + Population size*	5	5.94	<0.01
59	*Laying date + SST t-1 + Population size*	5	6.01	<0.01
60	*Laying date + Proportion of sandeel + Population size + February OC*	6	6.01	<0.01
61	*Laying date + Breeding OC + Population size + February OC*	6	6.03	<0.01
62	*Laying date + Proportion of sandeel + Breeding OC + February OC*	6	6.05	<0.01
63	*Laying date + Proportion of sandeel + SST t-1 + February OC + Laying date t-1*	7	6.22	<0.01
64	*Laying date + SST t-1 + February OC + February TP + Laying date t-1*	7	6.27	<0.01
65	*Laying date + SST t-1 + Breeding TP + February OC + Laying date t-1*	7	6.3	<0.01
66	*Laying date + SST t-1 + Population size + February OC + Laying date t-1*	7	6.36	<0.01

Rank	Model	k	ΔAICc	ω_i
67	*Laying date + SST t-1 + Breeding OC + February OC + Laying date t-1*	7	6.54	<0.01
68	*Laying date + SST + Breeding OC*	5	6.74	<0.01
69	*Laying date + SST + February TP*	5	6.82	<0.01
70	*Laying date + SST + Population size*	5	6.82	<0.01
71	*Laying date + SST + Proportion of sandeel*	5	6.85	<0.01
72	*Laying date + Breeding OC + February TP*	5	6.90	<0.01
73	*Laying date + Breeding OC + Population size*	5	6.91	<0.01
74	*Laying date + Breeding TP + Population size + Laying date t-1*	6	6.92	<0.01
75	*Laying date + Proportion of sandeel + Breeding OC*	5	6.96	<0.01
76	*Laying date + Breeding TP + Breeding OC + Laying date t-1*	6	6.97	<0.01
77	*Laying date + Population size + February TP*	5	6.99	<0.01

Table A14 Model selection table for detrended binomial Generalised Linear Mixed Models of breeding success between 1987-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. The best supported model is shown in **bold**, and models with equal support indicated with †.

Rank	Model	k	ΔAICc	ω_i
1	***Laying date + Laying date t-1 + Year***	**5**	**0.00**	**0.06**
2	*Laying date + Proportion of sandeel + Laying date t-1 + Year*	6	0.31	0.05
3†	*Laying date + February OC + Year*	5	0.50	0.05
4	*Laying date + Population size + February OC + Year*	6	1.09	0.04
5	*Laying date + Population size + Laying date t-1 + Year*	6	1.23	0.03
6†	*Laying date + Year*	4	1.68	0.03
7	*Laying date + Proportion of sandeel + Population size + Laying date t-1 + Year*	7	1.76	0.03
8	*Laying date + February OC + Laying date t-1 + Year*	6	1.85	0.02
9	*Laying date + Proportion of sandeel + February OC + Year*	6	2.41	0.02
10	*Laying date + SST t-1 + Laying date t-1 + Year*	6	2.41	0.02
11	*Laying date + Proportion of sandeel + SST t-1 + Laying date t-1 + Year*	7	2.52	0.02
12	*Laying date + Population size + February OC + Laying date t-1 + Year*	7	2.68	0.02
13	*Laying date + Breeding TP + Laying date t-1 + Year*	6	2.79	0.02
14	*Laying date + Proportion of sandeel + Year*	5	2.96	0.01
15	*Laying date + SST + Laying date t-1 + Year*	6	2.99	0.01
16	*Laying date + Proportion of sandeel + February OC + Laying date t-1 + Year*	7	3.05	0.01
17	*Laying date + Breeding OC + Laying date t-1 + Year*	6	3.14	0.01
18	*Laying date + February TP + Laying date t-1 + Year*	6	3.15	0.01
19	*Laying date + SST t-1 + February OC + Year*	6	3.22	0.01
20	*Laying date + Breeding TP + February OC + Year*	6	3.23	0.01
21	*Laying date + Population size + Year*	5	3.25	0.01
22	*Laying date + Proportion of sandeel + Population size + February OC + Year*	7	3.37	0.01
23	*Laying date + Proportion of sandeel + February TP + Laying date t-1 + Year*	7	3.42	0.01
24	*Laying date + Proportion of sandeel + Breeding OC + Laying date t-1 + Year*	7	3.58	0.01
25	*Laying date + SST + Proportion of sandeel + Laying date t-1 + Year*	7	3.60	0.01
26	*Laying date + February OC + February TP + Year*	6	3.61	0.01
27	*Laying date + Breeding OC + February OC + Year*	6	3.65	0.01

Rank	Model	k	ΔAICc	ω_i
28	*Laying date + Proportion of sandeel + Breeding TP + Laying date t-1 + Year*	7	3.71	0.01
29	*Laying date + Breeding TP + Year*	5	3.94	0.01
30	*Laying date + SST t-1 + Population size + Laying date t-1 + Year*	7	4.03	0.01
31	*Laying date + SST + Year*	5	4.05	0.01
32	*Laying date + February TP + Year*	5	4.16	0.01
33	*Laying date + SST t-1 + Population size + February OC + Year*	7	4.17	0.01
34	*Laying date + SST + Population size + Laying date t-1 + Year*	7	4.28	0.01
35	*Laying date + Proportion of sandeel + Population size + February OC + Laying date t-1 + Year*	8	4.30	0.01
36	*Laying date + Breeding TP + Population size + February OC + Year*	7	4.33	0.01
37	*Laying date + Breeding OC + Year*	5	4.39	0.01
38	*Laying date + Breeding OC + Population size + February OC + Year*	7	4.41	0.01
39	*Laying date + Proportion of sandeel + SST t-1 + Population size + Laying date t-1 + Year*	8	4.43	0.01
40	*Laying date + Population size + February OC + February TP + Year*	7	4.44	0.01
41	*Laying date + SST t-1 + Year*	5	4.44	0.01
42	*Laying date + Population size + February TP + Laying date t-1 + Year*	7	4.45	0.01
43	*Laying date + SST t-1 + February OC + Laying date t-1 + Year*	7	4.46	0.01
44	*Laying date + Breeding TP + Population size + Laying date t-1 + Year*	7	4.48	0.01
45	*Laying date + Breeding OC + Population size + Laying date t-1 + Year*	7	4.63	0.01
46	*Laying date + Proportion of sandeel + Population size + Year*	6	4.79	0.01
47	*Laying date + Breeding TP + February OC + Laying date t-1 + Year*	7	4.97	0.01
48	*Laying date + Population size + February TP + Year*	6	5.06	<0.01
49	*Laying date + February OC + February TP + Laying date t-1 + Year*	7	5.09	<0.01
50	*Laying date + SST + Proportion of sandeel + Population size + Laying date t-1 + Year*	8	5.15	<0.01
51	*Laying date + Proportion of sandeel + SST t-1 + February OC + Year*	7	5.27	<0.01
52	*Laying date + Breeding OC + February OC + Laying date t-1 + Year*	7	5.29	<0.01
53	*Laying date + SST + SST t-1 + Laying date t-1 + Year*	7	5.39	<0.01

Rank	Model	k	ΔAICc	ω_i
54	*Laying date + Proportion of sandeel + Breeding OC + Population size + Laying date t-1 + Year*	8	5.51	<0.01
55	*Laying date + Proportion of sandeel + Population size + February TP + Laying date t-1 + Year*	8	5.52	<0.01
56	*Laying date + Proportion of sandeel + Breeding TP + Population size + Laying date t-1 + Year*	8	5.52	<0.01
57	*Laying date + SST + Population size + Year*	6	5.53	<0.01
58	*Laying date + SST + Proportion of sandeel + Year*	6	5.56	<0.01
59	*Laying date + Proportion of sandeel + SST t-1 + February OC + Laying date t-1 + Year*	8	5.56	<0.01
60	*Laying date + Proportion of sandeel + Breeding OC + Year*	6	5.64	<0.01
61	*Laying date + Proportion of sandeel + February OC + February TP + Year*	7	5.65	<0.01
62	*Laying date + SST t-1 + Breeding TP + Laying date t-1 + Year*	7	5.66	<0.01
63	*Laying date + Proportion of sandeel + Breeding TP + February OC + Year*	7	5.67	<0.01
64	*Laying date + SST t-1 + Population size + February OC + Laying date t-1 + Year*	8	5.72	<0.01
65	*Laying date + Proportion of sandeel + Breeding OC + February OC + Year*	7	5.75	<0.01
66	*Laying date + SST + Proportion of sandeel + SST t-1 + Laying date t-1 + Year*	8	5.76	<0.01
67	*Laying date + SST t-1 + Breeding OC + Laying date t-1 + Year*	7	5.78	<0.01
68	*Laying date + Proportion of sandeel + Breeding TP + Year*	6	5.83	<0.01
69	*Laying date + SST t-1 + February TP + Laying date t-1 + Year*	7	5.85	<0.01
70	*Laying date + Proportion of sandeel + SST t-1 + Year*	6	5.86	<0.01
71	*Laying date + Proportion of sandeel + SST t-1 + Breeding OC + Laying date t-1 + Year*	8	5.92	<0.01
72	*Laying date + Breeding TP + Population size + Year*	6	5.94	<0.01
73	*Laying date + Proportion of sandeel + February TP + Year*	6	5.96	<0.01
74	*Laying date + Proportion of sandeel + SST t-1 + February TP + Laying date t-1 + Year*	8	5.99	<0.01
75	*Laying date + SST + Breeding TP + Laying date t-1 + Year*	7	6.10	<0.01
76	*Laying date + Proportion of sandeel + February OC + February TP + Laying date t-1 + Year*	8	6.10	<0.01
77	*Laying date + Breeding TP + Breeding OC + Laying date t-1 + Year*	7	6.16	<0.01
78	*Laying date + Breeding TP + February TP + Laying date t-1 + Year*	7	6.23	<0.01

Rank	Model	k	ΔAICc	ω_i
79	*Laying date + Breeding OC + Population size + February OC + Laying date t-1 + Year*	8	6.24	<0.01
80	*Laying date + Proportion of sandeel + SST t-1 + Breeding TP + Laying date t-1 + Year*	8	6.28	<0.01
81	*Laying date + SST t-1 + Population size + Year*	6	6.31	<0.01
82	*Laying date + Breeding TP + Population size + February OC + Laying date t-1 + Year*	8	6.32	<0.01
83	*Laying date + Breeding OC + Population size + Year*	6	6.36	<0.01
84	*Laying date + SST t-1 + Breeding TP + February OC + Year*	7	6.36	<0.01
85	*Laying date + SST + February TP + Laying date t-1 + Year*	7	6.41	<0.01
86	*Laying date + SST + Breeding OC + Laying date t-1 + Year*	7	6.41	<0.01
87	*Laying date + Population size + February OC + February TP + Laying date t-1 + Year*	8	6.44	<0.01
88	*Laying date + Breeding TP + February TP + Year*	6	6.50	<0.01
89	*Laying date + Breeding OC + February TP + Laying date t-1 + Year*	7	6.57	<0.01
90	*Laying date + Breeding TP + Breeding OC + February OC + Year*	7	6.62	<0.01
91	*Laying date + SST t-1 + Breeding OC + February OC + Year*	7	6.62	<0.01
92	*Laying date + SST t-1 + February OC + February TP + Year*	7	6.62	<0.01
93	*Laying date + Breeding TP + February OC + February TP + Year*	7	6.65	<0.01
94	*Laying date + SST + Breeding TP + Year*	6	6.65	<0.01
95	*Laying date + Proportion of sandeel + SST t-1 + Population size + February OC + Year*	8	6.66	<0.01
96	*Laying date + Breeding TP + Breeding OC + Year*	6	6.72	<0.01
97	*Laying date + Proportion of sandeel + Breeding OC + February OC + Laying date t-1 + Year*	8	6.74	<0.01
98	*Laying date + Proportion of sandeel + Breeding TP + February OC + Laying date t-1 + Year*	8	6.77	<0.01
99	*Laying date + SST + SST t-1 + Year*	6	6.81	<0.01
100	*Laying date + SST + February TP + Year*	6	6.93	<0.01
101	*Laying date + SST + Proportion of sandeel + February TP + Laying date t-1 + Year*	8	6.95	<0.01
102	*Laying date + Proportion of sandeel + Breeding OC + February TP + Laying date t-1 + Year*	8	6.98	<0.01

Table A15 Model selection table and effect sizes for GLMMs of breeding success, fitted with a Poisson error structure and a log(Population size) offset, between 1987-2016. OC = Onshore Component; t-1 = covariate lagged by one year. For model comparisons I present the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models. Due to the large number of potential models I only present those within 2 AICc of the top model. The best supported model is shown in bold, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	Est	SE	z	k	ΔAICc	ω_i
1	***Laying date + February OC***				**4**	**0.00**	**0.09**
	Laying date	**-0.49**	**0.07**	**-6.76**			
	February OC	**0.15**	**0.07**	**2.12**			
2	*Laying date + SST t-1 + February OC*				5	1.41	0.04
	Laying date	-0.52	0.07	-7.01			
	SST t-1	0.09	0.07	1.24			
	February OC	0.15	0.07	2.24			
3†	*Laying date*				3	1.55	0.04
	Laying date	-0.48	0.08	-6.19			

Table A16 Extended model selection table for Linear Models fitted for laying date between 1987-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparison the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ωi) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. The best supported model is shown in bold, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	k	ΔAICc	ω_i
1	***SST + SST t-1 + Breeding success t-1***	**5**	**0.00**	**0.23**
2	*SST + SST t-1 + Population size + Breeding success t-1*	6	0.51	0.18
3†	*SST t-1 + Breeding success t-1*	4	0.89	0.15
4†	*SST t-1 + Population size + Breeding success t-1*	5	1.4	0.11
5	*SST + SST t-1 + February TP + Breeding success t-1*	6	2.58	0.06
6	*SST t-1 + February TP + Breeding success t-1*	5	3.36	0.04
7	*SST t-1 + February OC + Breeding success t-1*	5	3.54	0.04
8	*SST + SST t-1 + Population size + February TP + Breeding success t-1*	7	3.65	0.04
9	*SST t-1 + Population size + February OC + Breeding success t-1*	6	4.13	0.03
10	*SST t-1 + Population size + February TP + Breeding success t-1*	6	4.35	0.03
11	*Breeding success t-1*	3	4.37	0.03
12	*February TP + Breeding success t-1*	4	5.88	0.01
13	*SST + Breeding success t-1*	4	6.06	0.01
14	*SST t-1 + February OC + February TP + Breeding success t-1*	6	6.08	0.01
15	*Population size + Breeding success t-1*	4	6.78	0.01
16	*February OC + Breeding success t-1*	4	6.99	0.01

Table A17 Model selection table for detrended Linear Models of laying date modelled between 1986-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. The best supported model is shown in **bold**.

Rank	Model	k	ΔAICc	ω_i
1	***SST t-1 + Breeding success t-1 + Year***	**4**	**0.00**	**0.21**
2	*SST + SST t-1 + Breeding success t-1 + Year*	5	0.51	0.16
3	*SST t-1 + February TP + Breeding success t-1 + Year*	5	2.34	0.07
4	*SST t-1 + Population size + Breeding success t-1 + Year*	5	2.38	0.06
5	*SST t-1 + February OC + Breeding success t-1 + Year*	5	2.77	0.05
6	*SST + SST t-1 + February TP + Breeding success t-1 + Year*	6	3.01	0.05
7	*SST + SST t-1 + Population size + Breeding success t-1 + Year*	6	3.59	0.03
8	*SST t-1 + Population size + February TP + Breeding success t-1 + Year*	6	4.26	0.03
9	*SST + SST t-1 + Breeding success t-1*	4	4.26	0.02
10	*SST t-1 + Population size + Year*	4	4.33	0.02
11	*SST + SST t-1 + Population size + Breeding success t-1*	5	4.77	0.02
12	*SST t-1 + Year*	3	4.81	0.02
13	*SST t-1 + Population size + February TP + Year*	5	5.05	0.02
14	*SST t-1 + February OC + February TP + Breeding success t-1 + Year*	6	5.07	0.02
15	*SST t-1 + Breeding success t-1*	3	5.15	0.02
16	*SST + SST t-1 + Year*	4	5.38	0.01
17	*SST t-1 + Population size + February OC + Breeding success t-1 + Year*	6	5.52	0.01
18	*SST t-1 + Population size + Breeding success t-1*	4	5.66	0.01
19	*SST + SST t-1 + Population size + February TP + Breeding success t-1 + Year*	7	5.86	0.01
20	*SST + SST t-1 + Population size + Year*	5	5.94	0.01
21	*SST t-1 + Population size + February TP + Laying date t-1 + Year*	6	6.37	0.01
22	*SST t-1 + Laying date t-1 + Year*	4	6.54	0.01
23	*SST t-1 + Population size + Laying date t-1 + Year*	5	6.61	0.01
24	*SST t-1 + February OC + Year*	4	6.64	0.01
25	*SST t-1 + February TP + Year*	4	6.82	0.01
26	*SST + SST t-1 + February TP + Breeding success t-1*	5	6.85	0.01
27	*SST t-1 + Population size + February OC + Year*	5	6.89	0.01
28	*SST + SST t-1 + Population size + February TP + Year*	6	6.98	0.01

APPENDIX 3.3 EXTENDED MODEL SELECTION TABLE FITTED FOR BROOD SIZE

Table A18 Extended model selection table for binomial Generalised Linear Mixed Effect Models fitted for brood size, modelled between 1974-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparison the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. Best supported model shown in **bold**.

Rank	Model	k	ΔAICc	ω_i
1	***Ringing date + February OC***	**4**	**0.00**	**0.09**
2	*Ringing date + Breeding TP + February OC*	5	0.85	0.06
3	*Ringing date + February OC + Brood size t-1*	5	1.7	0.04
4	*Ringing date + Breeding OC + February OC*	5	2.11	0.03
5	*Ringing date + SST t-1 + February OC*	5	2.25	0.03
6	*Ringing date + February OC + February TP*	5	2.44	0.03
7	*Ringing date + Breeding TP + February OC + Brood size t-1*	6	2.48	0.03
8	*Ringing date + February OC + Ringing date t-1*	5	2.49	0.03
9	*Ringing date + Population size + February OC*	5	2.57	0.02
10	*Ringing date + Breeding TP*	4	3.01	0.02
11	*Ringing date + Breeding TP + Breeding OC + February OC*	6	3.14	0.02
12	*Ringing date*	3	3.32	0.02
13	*Ringing date + Breeding TP + February OC + Ringing date t-1*	6	3.40	0.02
14	*Ringing date + SST t-1 + Breeding TP + February OC*	6	3.43	0.02
15	*Ringing date + Breeding TP + Population size + February OC*	6	3.54	0.02
16	*Ringing date + Breeding TP + February OC + February TP*	6	3.56	0.01
17	*Ringing date + Breeding TP + Ringing date t-1*	5	3.62	0.01
18	*Ringing date + SST*	4	3.82	0.01
19	*Ringing date + Ringing date t-1*	4	3.84	0.01
20	*Ringing date + Breeding OC + February OC + Brood size t-1*	6	4.06	0.01
21	*Ringing date + SST t-1 + February OC + Brood size t-1*	6	4.16	0.01
22	*Ringing date + SST + Breeding TP*	5	4.29	0.01
23	*Ringing date + February OC + February TP + Brood size t-1*	6	4.36	0.01
24	*Ringing date + Population size + February OC + Brood size t-1*	6	4.41	0.01
25	*Ringing date + SST t-1 + Breeding OC + February OC*	6	4.54	0.01
26	*Ringing date + Breeding OC + February OC + Ringing date t-1*	6	4.67	0.01
27	*Ringing date + Breeding OC + February OC + February TP*	6	4.70	0.01
28	*Ringing date + SST t-1 + February OC + Ringing date t-1*	6	4.76	0.01
29	*Ringing date + Breeding OC + Population size + February OC*	6	4.81	0.01
30	*Ringing date + SST t-1 + Population size + February OC*	6	4.88	0.01

Rank	Model	k	ΔAICc	ω_i
31	*Ringing date + SST t-1 + February OC + February TP*	6	4.89	0.01
32	*Ringing date + February OC + February TP + Ringing date t-1*	6	4.94	0.01
33	*Ringing date + Breeding TP + Breeding OC + February OC + Brood size t-1*	7	5.04	0.01
34	*Ringing date + Breeding TP + Brood size t-1*	5	5.11	0.01
35	*Ringing date + Population size + February OC + February TP*	6	5.15	0.01
36	*Ringing date + Population size + February OC + Ringing date t-1*	6	5.20	0.01
37	*Ringing date + SST + Ringing date t-1*	5	5.21	0.01
38	*Ringing date + Breeding TP + February TP*	5	5.24	0.01
39	*Ringing date + SST t-1 + Breeding TP + February OC + Brood size t-1*	7	5.27	0.01
40	*Ringing date + Breeding TP + February OC + February TP + Brood size t-1*	7	5.32	0.01
41	*Ringing date + Breeding TP + Population size + February OC + Brood size t-1*	7	5.34	0.01
42	*Ringing date + SST t-1 + Breeding TP*	5	5.41	0.01
43	*Ringing date + Breeding TP + Population size*	5	5.44	0.01
44	*Ringing date + Brood size t-1*	4	5.50	0.01
45	*Ringing date + Breeding TP + Breeding OC*	5	5.52	0.01
46	*Ringing date + SST + Breeding TP + Ringing date t-1*	6	5.65	0.01
47	*Ringing date + SST t-1*	4	5.69	0.01
48	*Ringing date + February TP*	4	5.69	0.01
49	*Ringing date + Population size*	4	5.70	0.01
50	*Ringing date + Breeding OC*	4	5.70	0.01
51	*Ringing date + Breeding TP + Breeding OC + February OC + Ringing date t-1*	7	5.74	0.01
52	*Ringing date + SST t-1 + Breeding TP + Breeding OC + February OC*	7	5.89	<0.01
53	*Ringing date + Breeding TP + Breeding OC + Population size + February OC*	7	5.95	<0.01
54	*Ringing date + Breeding TP + Breeding OC + February OC + February TP*	7	6.00	<0.01
55	*Ringing date + Breeding TP + Breeding OC + Ringing date t-1*	6	6.02	<0.01
56	*Ringing date + SST t-1 + Breeding TP + February OC + Ringing date t-1*	7	6.03	<0.01
57	*Ringing date + Breeding OC + Ringing date t-1*	5	6.12	<0.01
58	*Ringing date + SST t-1 + Breeding TP + Population size + February OC*	7	6.19	<0.01
59	*Ringing date + Breeding TP + February OC + February TP + Ringing date t-1*	7	6.22	<0.01
60	*Ringing date + Breeding TP + Population size + February OC + Ringing date t-1*	7	6.25	<0.01
61	*Ringing date + SST + Brood size t-1*	5	6.25	<0.01

Rank	Model	k	ΔAICc	ω_i
62	*Ringing date + February TP + Ringing date t-1*	5	6.25	<0.01
63	*Ringing date + Breeding TP + Population size + Ringing date t-1*	6	6.29	<0.01
64	*Ringing date + SST t-1 + Breeding TP + February OC + February TP*	7	6.30	<0.01
65	*Ringing date + SST + SST t-1*	5	6.30	<0.01
66	*Ringing date + SST t-1 + Breeding TP + Ringing date t-1*	6	6.31	<0.01
67	*Ringing date + SST t-1 + Ringing date t-1*	5	6.33	<0.01
68	*Ringing date + Breeding TP + February TP + Ringing date t-1*	6	6.33	<0.01
69	*Ringing date + SST + February TP*	5	6.34	<0.01
70	*Ringing date + SST + Breeding OC*	5	6.35	<0.01
71	*Ringing date + SST + Population size*	5	6.39	<0.01
72	*Ringing date + Breeding TP + Population size + February OC + February TP*	7	6.40	<0.01
73	*Ringing date + Population size + Ringing date t-1*	5	6.40	<0.01
74	*Ringing date + SST + Breeding TP + Brood size t-1*	6	6.69	<0.01
75	*Ringing date + SST t-1 + Breeding OC + February OC + Brood size t-1*	7	6.70	<0.01
76	*Ringing date + SST + Breeding TP + February TP*	6	6.72	<0.01
77	*Ringing date + Breeding OC + February OC + February TP + Brood size t-1*	7	6.88	<0.01
78	*Ringing date + Breeding OC + Population size + February OC + Brood size t-1*	7	6.93	<0.01
79	*Ringing date + SST + Breeding TP + Breeding OC*	6	6.95	<0.01
80	*Ringing date + SST + Breeding TP + Population size*	6	6.98	<0.01
81	*Ringing date + SST t-1 + Population size + February OC + Brood size t-1*	7	6.99	<0.01

APPENDIX 3.4 EXTENDED MODEL SELECTION TABLE FOR MODELS OF RINGING DATE

Table A19 Extended model selection table for Linear Models fitted for ringing date, modelled between 1974-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparison the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Only models within 7 AIC care presented. Best supported model shown in **bold**, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	k	ΔAICc	ω_i
1	***SST + SST t-1 + Brood size t-1***	**5**	**0.00**	**0.20**
2	*SST + SST t-1 + Population size + Brood size t-1*	6	1.11	0.12
3†	*SST + Brood size t-1*	4	1.24	0.11
4	*SST + SST t-1 + February TP + Brood size t-1*	6	2.00	0.07
5	*SST + February TP + Brood size t-1*	5	2.03	0.07
6	*Brood size t-1*	3	3.44	0.04
7	*SST + Population size + Brood size t-1*	5	3.55	0.03
8	*SST + SST t-1 + Population size + February TP + Brood size t-1*	7	3.67	0.03
9	*February OC + February TP + Brood size t-1*	5	3.84	0.03
10	*February OC + Brood size t-1*	4	4.04	0.03
11	*February TP + Brood size t-1*	4	4.11	0.03
12	*SST t-1 + February OC + Brood size t-1*	5	4.18	0.02
13	*SST t-1 + Population size + February OC + Brood size t-1*	6	4.61	0.02
14	*SST + Population size + February TP + Brood size t-1*	6	4.63	0.02
15	*SST t-1 + Brood size t-1*	4	4.72	0.02
16	*Population size + Brood size t-1*	4	4.95	0.02
17	*SST t-1 + February OC + February TP + Brood size t-1*	6	4.98	0.02
18	*SST t-1 + Population size + Brood size t-1*	5	5.05	0.02
19	*Population size + February OC + Brood size t-1*	5	5.94	0.01
20	*Population size + February TP + Brood size t-1*	5	6.04	0.01
21	*SST t-1 + February TP + Brood size t-1*	5	6.09	0.01
22	*Population size + February OC + February TP + Brood size t-1*	6	6.24	0.01
23	*SST t-1 + Population size + February OC + February TP + Brood size t-1*	7	6.41	0.01

APPENDIX 3.5 CORRELATION BETWEEN EXPLANATORY COVARIATES OF BROOD SIZE AND RINGING DATE

Table A20 Pearson's correlation coefficients between each of the explanatory covariates used in the model selection process of brood size and ringing date between 1974 and 2016. Highly correlated variables (R > 0.60) are indicated in **bold**.

	Brood size t-1	**Ringing date t-1**	**February OC**	**February TP**	**Breeding OC**	**Breeding TP**	**SST**	**SST t-1**	**Population size**	**Ringing date**
Brood size t-1										
Ringing date t-1	**-0.68**									
February OC	-0.31	0.57								
February TP	-0.09	0.37	0.21							
Breeding OC	0.09	0.07	0.05	0.14						
Breeding OC	0.15	-0.05	-0.21	0.19	0.04					
SST	0.09	-0.34	**-0.67**	0.02	0.15	0.22				
SST t-1	0.04	-0.32	-0.28	-0.26	-0.13	-0.10	0.31			
Population size	0.01	0.15	0.12	-0.14	0.04	0.07	-0.23	-0.37		
Ringing date	-0.49	0.35	0.32	-0.13	-0.35	-0.10	-0.32	0.12	0.12	

APPENDIX 3.6 EXTENDED MODEL SELECTION TABLE FOR DETRENDED MODELS OF BROOD SIZE

Table A21 Model selection table for detrended binomial Generalised Linear Mixed Models of brood size modelled between 1974-2016. Ringing date = Ringing date; February OC = February OC; Breeding TP = breeding total precipitation; Population size = population size; Breeding OC = breeding OC; SST = Sea Surface Temperature; and February TP = February total precipitation. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. Best supported model shown in **bold**.

Rank	Model	k	ΔAICc	ω_i
1	***Ringing date + February OC + Year***	**4**	**0.00**	**0.10**
2	*Ringing date + Population size + February OC + Year*	5	0.91	0.06
3	*Ringing date + Breeding TP + February OC + Year*	5	1.26	0.05
4	*Ringing date + February OC + Brood size t-1 + Year*	5	1.87	0.04
5	*Ringing date + Breeding TP + Population size + February OC + Year*	6	2.15	0.03
6	*Ringing date + Breeding OC + February OC + Year*	5	2.22	0.03
7	*Ringing date + February OC + Ringing date t-1 + Year*	5	2.42	0.03
8	*Ringing date + February OC + February TP + Year*	5	2.66	0.03
9	*Ringing date + SST t-1 + February OC + Year*	5	2.69	0.03
10	*Ringing date + Breeding OC + Population size + February OC + Year*	6	3.01	0.02
11	*Ringing date + Breeding TP + February OC + Brood size t-1 + Year*	6	3.09	0.02
12	*Ringing date + Population size + February OC + Brood size t-1 + Year*	6	3.22	0.02
13	*Ringing date + Population size + February OC + Ringing date t-1 + Year*	6	3.45	0.02
14	*Ringing date + Breeding TP + Breeding OC + February OC + Year*	6	3.67	0.02
15	*Ringing date + Breeding TP + February OC + Ringing date t-1 + Year*	6	3.71	0.02
16	*Ringing date + Population size + February OC + February TP + Year*	6	3.74	0.01
17	*Ringing date + SST t-1 + Population size + February OC + Year*	6	3.77	0.01
18	*Ringing date + SST t-1 + Breeding TP + February OC + Year*	6	4.02	0.01

Rank	Model	k	ΔAICc	ω_i
19	*Ringing date + Breeding TP + February OC + February TP + Year*	6	4.12	0.01
20	*Ringing date + Breeding OC + February OC + Brood size t-1 + Year*	6	4.36	0.01
21	*Ringing date + Breeding TP + Breeding OC + Population size + February OC + Year*	7	4.44	0.01
22	*Ringing date + Breeding TP + Population size + February OC + Brood size t-1 + Year*	7	4.48	0.01
23	*Ringing date + SST + Year*	4	4.66	0.01
24	*Ringing date + Breeding OC + February OC + Ringing date t-1 + Year*	6	4.66	0.01
25	*Ringing date + SST t-1 + February OC + Brood size t-1 + Year*	6	4.69	0.01
26	*Ringing date + Breeding TP + Population size + February OC + Ringing date t-1 + Year*	7	4.72	0.01
27	*Ringing date + February OC + February TP + Brood size t-1 + Year*	6	4.73	0.01
28	*Ringing date + Breeding TP + Year*	4	4.83	0.01
29	*Ringing date + Breeding TP + Population size + February OC + February TP + Year*	7	4.89	0.01
30	*Ringing date + Breeding TP + Ringing date t-1 + Year*	5	4.94	0.01
31	*Ringing date + Ringing date t-1 + Year*	4	4.97	0.01
32	*Ringing date + Year*	3	4.97	0.01
33	*Ringing date + Breeding OC + February OC + February TP + Year*	6	5.05	0.01
34	*Ringing date + SST t-1 + Breeding OC + February OC + Year*	6	5.05	0.01
35	*Ringing date + February OC + February TP + Ringing date t-1 + Year*	6	5.07	0.01
36	*Ringing date + SST t-1 + Breeding TP + Population size + February OC + Year*	7	5.14	0.01
37	*Ringing date + SST t-1 + February OC + Ringing date t-1 + Year*	6	5.29	0.01
38	*Ringing date + SST + Ringing date t-1 + Year*	5	5.42	0.01
39	*Ringing date + SST t-1 + February OC + February TP + Year*	6	5.48	0.01
40	*Ringing date + SST + Breeding TP + Year*	5	5.52	0.01
41	*Ringing date + Breeding OC + Population size + February OC + Ringing date t-1 + Year*	7	5.52	0.01
42	*Ringing date + Breeding OC + Population size + February OC + Brood size t-1 + Year*	7	5.62	0.01
43	*Ringing date + Breeding TP + Breeding OC + February OC + Brood size t-1 + Year*	7	5.79	0.01
44	*Ringing date + SST t-1 + Breeding TP + February OC + Brood size t-1 + Year*	7	5.96	<0.01

Rank	Model	k	ΔAICc	ω_i
45	*Ringing date + Breeding OC + Population size + February OC + February TP + Year*	7	5.98	<0.01
46	*Ringing date + SST t-1 + Breeding OC + Population size + February OC + Year*	7	6.03	<0.01
47	*Ringing date + Breeding TP + February OC + February TP + Brood size t-1 + Year*	7	6.06	<0.01
48	*Ringing date + Breeding TP + Breeding OC + February OC + Ringing date t-1 + Year*	7	6.13	<0.01
49	*Ringing date + Population size + February OC + February TP + Brood size t-1 + Year*	7	6.18	<0.01
50	*Ringing date + SST t-1 + Population size + February OC + Brood size t-1 + Year*	7	6.25	<0.01
51	*Ringing date + SST + Breeding TP + Ringing date t-1 + Year*	6	6.31	<0.01
52	*Ringing date + SST t-1 + Population size + February OC + Ringing date t-1 + Year*	7	6.48	<0.01
53	*Ringing date + Population size + February OC + February TP + Ringing date t-1 + Year*	7	6.48	<0.01
54	*Ringing date + SST t-1 + Breeding TP + Breeding OC + February OC + Year*	7	6.57	<0.01
55	*Ringing date + SST + Population size + Year*	5	6.68	<0.01
56	*Ringing date + Breeding TP + Breeding OC + February OC + February TP + Year*	7	6.7	<0.01
57	*Ringing date + SST t-1 + Breeding TP + February OC + Ringing date t-1 + Year*	7	6.71	<0.01
58	*Ringing date + Breeding TP + February OC + February TP + Ringing date t-1 + Year*	7	6.71	<0.01
59	*Ringing date + Breeding TP + Population size + Ringing date t-1 + Year*	6	6.76	<0.01
60	*Ringing date + SST t-1 + Population size + February OC + February TP + Year*	7	6.78	<0.01
61	*Ringing date + Breeding TP + Population size + Year*	5	6.83	<0.01
62	*Ringing date + Population size + Ringing date t-1 + Year*	5	6.92	<0.01
63	*Ringing date + SST t-1 + Breeding TP + Year*	5	6.94	<0.01
64	*Ringing date + Breeding TP + Breeding OC + Population size + February OC + Ringing date t-1 + Year*	8	6.97	<0.01

APPENDIX 3.7 EXTENDED MODEL SELECTION TABLE FOR DETRENDED MODELS OF RINGING DATE

Table A22 Model selection table for detrended Linear Models of ringing date modelled between 1974-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ωi) relative to all models are presented for each model. Due to the large number of potential models I only present those within 7 AICc of the top model. Best supported model shown in **bold**.

Rank	Model	k	ΔAICc	ω_i
1	***SST t-1 + Brood size t-1 + Year***	**5**	**0.00**	**0.17**
2	*SST + SST t-1 + Brood size t-1 + Year*	6	0.16	0.16
3	*SST t-1 + February TP + Brood size t-1 + Year*	6	1.31	0.09
4	*SST + SST t-1 + February TP + Brood size t-1 + Year*	7	1.96	0.06
5	*SST t-1 + Population size + Brood size t-1 + Year*	6	1.96	0.06
6	*SST t-1 + February OC + Brood size t-1 + Year*	6	2.18	0.06
7	*SST + SST t-1 + Population size + Brood size t-1 + Year*	7	2.47	0.05
8	*SST t-1 + Population size + February TP + Brood size t-1 + Year*	7	2.48	0.05
9	*SST t-1 + February OC + February TP + Brood size t-1 + Year*	7	3.31	0.03
10	*SST + SST t-1 + Population size + February TP + Brood size t-1 + Year*	8	3.70	0.03
11	*SST t-1 + Population size + February OC + Brood size t-1 + Year*	7	4.49	0.02
12	*Population size + February TP + Brood size t-1 + Year*	6	4.84	0.02
13	*SST t-1 + Ringing date t-1 + Year*	5	4.89	0.01
14	*SST t-1 + Population size + February OC + February TP + Brood size t-1 + Year*	8	4.94	0.01
15	*SST t-1 + February TP + Ringing date t-1 + Year*	6	4.97	0.01
16	*SST t-1 + Population size + February TP + Ringing date t-1 + Year*	7	5.02	0.01
17	*February TP + Brood size t-1 + Year*	5	5.42	0.01
18	*Brood size t-1 + Year*	4	5.97	0.01
19	*SST t-1 + Year*	4	6.05	0.01
20	*SST t-1 + Population size + Ringing date t-1 + Year*	6	6.37	0.01
21	*SST + SST t-1 + Ringing date t-1 + Year*	6	6.40	0.01
22	*SST t-1 + Population size + Year*	5	6.73	0.01
23	*SST + SST t-1 + Year*	5	6.78	0.01
24	*SST t-1 + February OC + Year*	5	6.91	0.01
25	*Population size + Brood size t-1 + Year*	5	6.95	0.01

APPENDIX 3.8 MODEL SELECTION TABLE FOR POISSON MODEL OF BROOD SIZE

Table A23 Model selection table and effect sizes for GLMMs of brood size, fitted with a Poisson error structure and a log(Population size) offset, between 1974-2016. OC = Onshore Component; TP = Total Precipitation, t-1 = covariate lagged by one year. For each fixed effect within a model, I report an estimate (± SE) and z-value For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Only models within 2 AICc points of the top model presented. Best supported model shown in **bold**.

Rank	Model	Est	SE	z	k	ΔAICc	ω_i
1	***Ringing date + February OC***				**5**	**0.00**	**0.10**
	Ringing date	**-0.09**	**0.01**	**-6.38**			
	February OC	**0.04**	**0.01**	**2.52**			
2	*Ringing date + Breeding TP + February OC*				6	0.95	0.06
	Ringing date	-0.09	0.01	-6.52			
	Breeding TP	-0.02	0.01	-1.29			
	February OC	0.03	0.01	2.29			

APPENDIX 3.9 MODEL SELECTION TABLE FOR SUPPLEMENTARY DIET ANALYSIS OF BROOD SIZE

Table A24 Model selection table and effect sizes for supplementary diet analysis of brood size. Models fitted with fitting binomial GLMMs and a logit-link function, between 1985-2016. OC = Onshore Component. For each fixed effect within a model, I report an estimate (± SE) and z-value. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Only models within 2 AICc points of the top model presented. Best supported model shown in **bold**, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	Est	SE	z	k	ΔAICc	ω_i
1	***Ringing date + February OC***				**4**	**0.00**	**0.53**
	Ringing date	**-0.10**	**0.02**	**-5.46**			
	February OC	**0.04**	**0.02**	**2.20**			
2†	*Ringing date*				3	1.93	0.20
	Ringing date	-0.09	0.02	-4.78			

APPENDIX 3.10 MODEL SELECTION TABLE FOR SUPPLEMENTARY DETRENDED DIET ANALYSIS OF BROOD SIZE

Table A25 Model selection table and effect sizes for supplementary detrended diet analysis of brood size. Models fitted with fitting binomial GLMMs and a logit-link function, between 1986-2016. OC = Onshore Component; t-1 = covariate lagged by one year. For model comparisons the number of parameters (k), difference in AICc relative to best supported model (ΔAICc) and model weight (ω_i) relative to all models are presented for each model. Due to the large number of potential models I only present those within 2 AICc of the top model. Best supported model shown in **bold**, and models with strong support (<2 AICc and same number of parameters or less) indicated with †.

Rank	Model	Est	SE	z	k	ΔAICc	ω_i
1	***Ringing date + Proportion of sandeel***				**6**	**0.00**	**0.49**
	+ February OC + Year						
	Ringing date	**-0.06**	**0.02**	**-2.98**			
	Proportion of sandeel	**0.05**	**0.02**	**2.32**			
	February OC	**0.04**	**0.02**	**2.25**			
	Year	**0.06**	**0.02**	**2.52**			
2†	*Ringing date + Proportion of sandeel + Year*				5	1.75	0.28
	Ringing date	-0.06	0.02	-2.47			
	Proportion of sandeel	0.05	0.02	2.43			
	Year	0.06	0.03	2.35			

Appendix 4

APPENDIX 4.1 SUPPLEMENTARY ANALYSIS OF ALL NESTING EVENTS

In order to investigate whether my results differed between all breeding events and all nesting attempts, which included preliminary nesting activity (site occupancy and nest building), the following analysis was undertaken.

The total number of all nesting events was 12,399 (mean annual number of all nesting events ± SD: 564 ± 177; 349–1022). Over the study, the annual mean (± SD) nest site distance along coastline of all nesting attempts was 3875 m ± 280 m (range: 2987–3875 m). The total number of all nesting events on the south-west and north-east side of the island respectively was 4673 (annual mean number on west ± SD: 21 ± 88; range: 109–414) and 7726 (annual mean number on east ± SD: 351 ± 97; range: 215–608). The annual mean proportion of all failed nests on the south-west side of the island (± SD) was 0.37 ± 0.06 (range: 0.28–0.47).

For all nesting events, overlap in usage closely matched that of all breeding events (Figure A4). The mean annual pairwise overlap of the core nesting areas (50%) for all failed nests was 0.73 ± 0.11 (range: 0.49–0.94; Table A26; Figure A4).

The trend in the annual mean distance along coastline for all nesting events changed from 3,268.80 m in 1994 to 1,167.82 m in 2015 (Table A27; Figure A5a). The proportion of all nesting events on the south-west side was consistently lower over the study, but reduced from 0.46 in 1994 to 0.28 in 2015 (Table A27; Figure A5b, c).

Table A26 Pairwise Bhattacharyya's affinity for core areas (50%) of all nesting events between years.

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1994	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
1995	0.78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1996	0.76	0.87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1997	0.75	0.82	0.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1998	0.73	0.84	0.90	0.88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1999	0.71	0.78	0.86	0.85	0.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2000	0.72	0.86	0.92	0.87	0.92	0.88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2001	0.73	0.82	0.89	0.83	0.88	0.86	0.94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2002	0.70	0.80	0.78	0.76	0.82	0.79	0.85	0.90	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2003	0.68	0.73	0.73	0.78	0.72	0.81	0.78	0.81	0.85	-	-	-	-	-	-	-	-	-	-	-	-	-
2004	0.71	0.72	0.71	0.76	0.69	0.75	0.77	0.83	0.80	0.87	-	-	-	-	-	-	-	-	-	-	-	-
2005	0.53	0.54	0.58	0.60	0.57	0.68	0.66	0.74	0.75	0.82	0.82	-	-	-	-	-	-	-	-	-	-	-
2006	0.61	0.61	0.61	0.70	0.58	0.69	0.68	0.74	0.68	0.81	0.88	0.85	-	-	-	-	-	-	-	-	-	-
2007	0.60	0.66	0.64	0.70	0.57	0.67	0.67	0.70	0.64	0.82	0.84	0.82	0.94	-	-	-	-	-	-	-	-	-
2008	0.54	0.60	0.58	0.65	0.52	0.61	0.62	0.64	0.58	0.76	0.78	0.76	0.91	0.93	-	-	-	-	-	-	-	-
2009	0.58	0.68	0.66	0.68	0.60	0.65	0.70	0.72	0.66	0.80	0.82	0.80	0.88	0.93	0.87	-	-	-	-	-	-	-
2010	0.57	0.62	0.65	0.63	0.58	0.68	0.68	0.71	0.69	0.82	0.78	0.83	0.82	0.87	0.86	0.89	-	-	-	-	-	-
2011	0.59	0.65	0.63	0.64	0.56	0.65	0.66	0.68	0.69	0.86	0.81	0.79	0.82	0.87	0.86	0.89	0.94	-	-	-	-	-
2012	0.59	0.59	0.57	0.63	0.51	0.60	0.61	0.68	0.67	0.79	0.82	0.75	0.86	0.87	0.85	0.82	0.84	0.88	-	-	-	-
2013	0.59	0.68	0.65	0.68	0.59	0.58	0.68	0.70	0.68	0.77	0.79	0.68	0.75	0.8	0.83	0.86	0.84	0.89	0.83	-	-	-
2014	0.54	0.59	0.60	0.59	0.54	0.49	0.62	0.64	0.59	0.68	0.70	0.60	0.68	0.73	0.72	0.79	0.77	0.82	0.75	0.85	-	-
2015	0.64	0.63	0.66	0.64	0.59	0.55	0.68	0.73	0.64	0.65	0.72	0.66	0.71	0.72	0.71	0.79	0.78	0.79	0.75	0.81	0.90	-

Table A27 Model selection table for circular Linear Models testing for temporal trends in annual mean distance along coastline and binomial Generalised Linear Mixed Models for temporal trends in nest aspect for all nesting events. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z/t values, number of parameters (k), difference in AICc between top model and selected model (Δ AICc) and Akaike weight relative to other models (ωi). Top models are shown in **bold**.

Response	Rank	Model	Est	SE	t/z	k	Δ AICc	ω_i
Distance along coastline	**1**	***year***				**2**	**0.00**	**1.00**
		year	**-0.34**	**0.05**	**-6.3**			
	2	*i*				1	27.23	<0.01
Island side	**1**	***year***				**2**	**0.00**	**1.00**
		year	**-0.24**	**0.028**	**-8.62**			
	2	*i*				1	30.26	<0.01

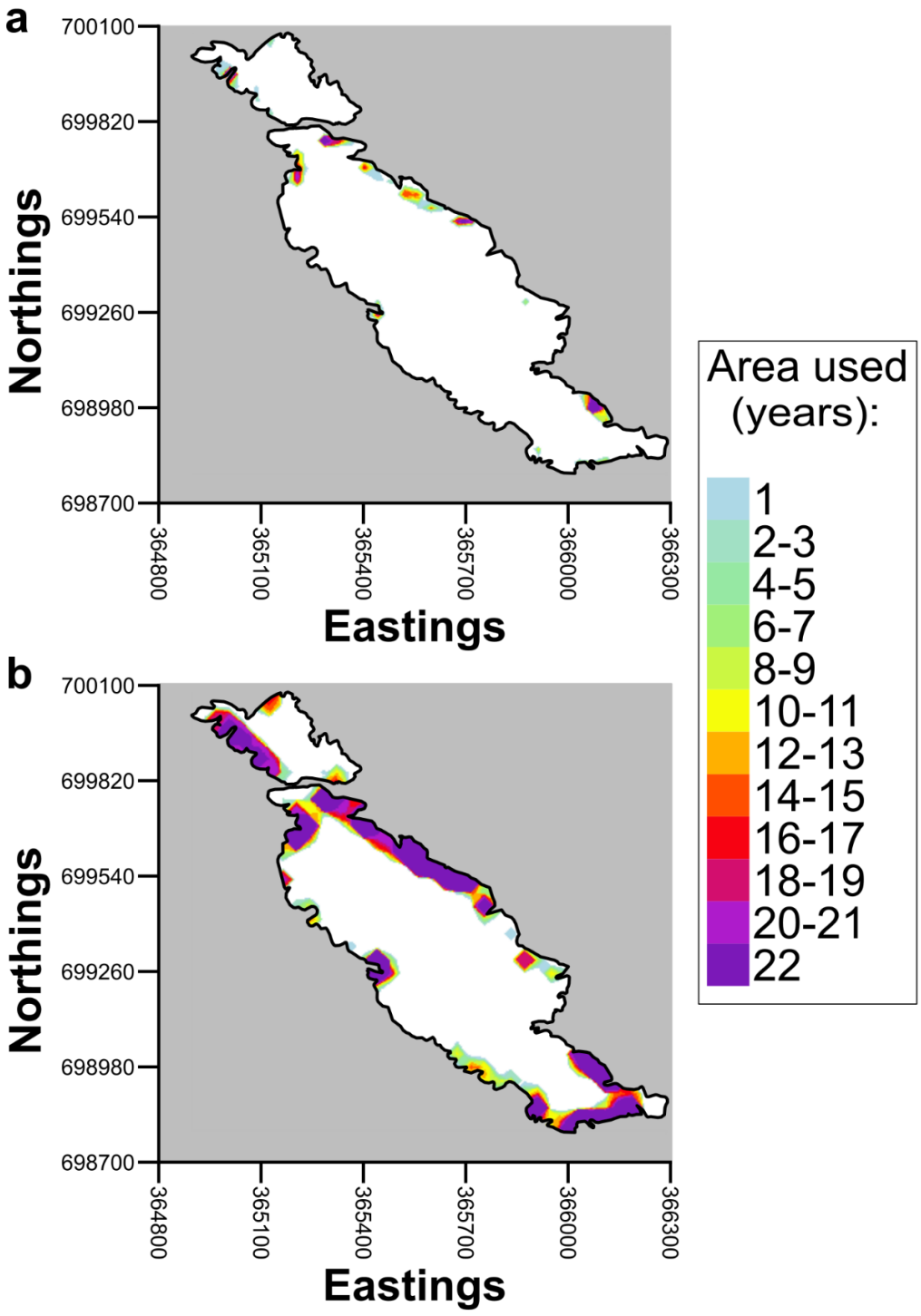

Figure A4 Consistency in nesting distribution within the a) core area (50%) and b) area of active use (95%) for all nesting events. Areas used indicates number of years core areas overlap between years.

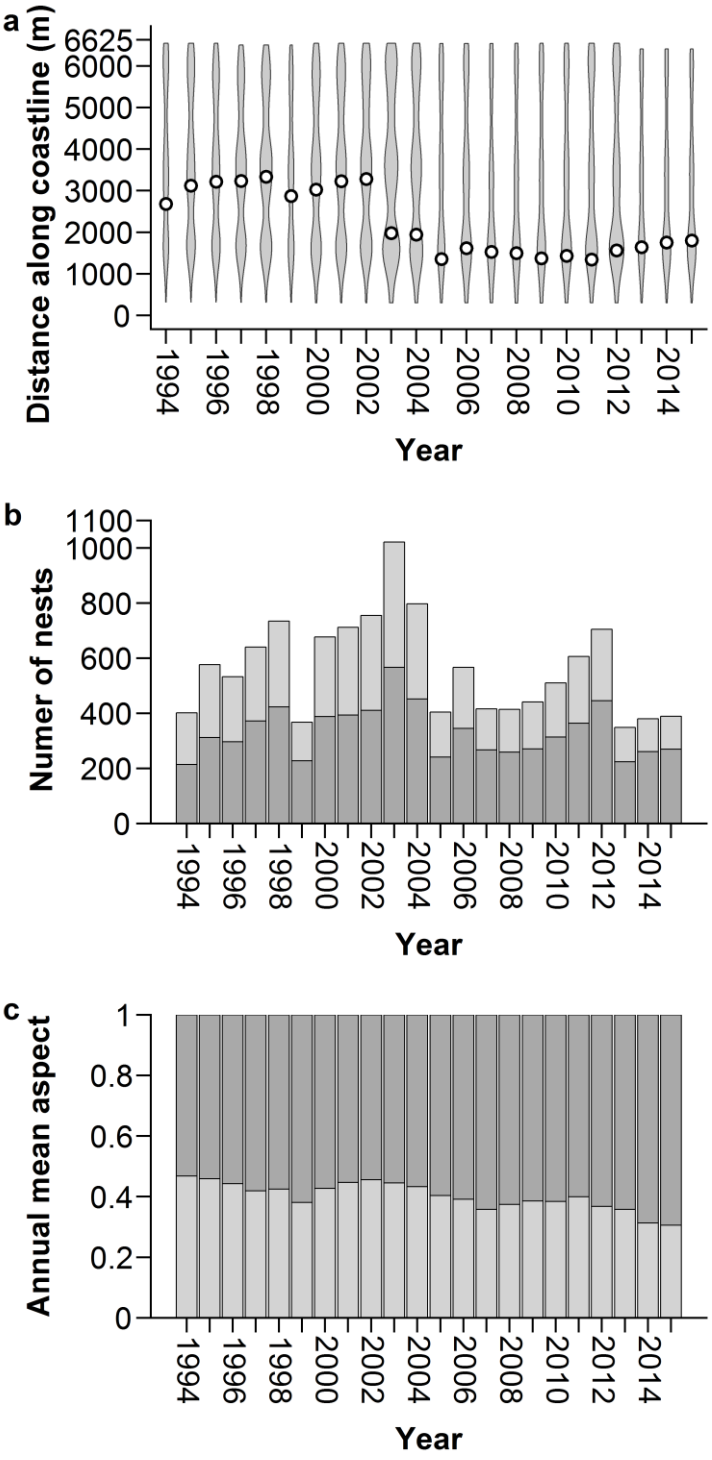

Figure A5 Violin plots displaying interannual variation in distance along coastline between 1994 and 2015 for all nesting events. The violin plot for each year is scaled relative to the number of nests present. Annual circular mean indicated with open circles (○); b) interannual variation in total number of nests on the south-west (light grey) and north-east (dark grey) side of the island between 1994 and 2015 for all nesting events, and c) interannual variation in the proportion of south-western (light-grey) and north-eastern nests (dark grey) between 1994 and 2015 for all nesting events.

APPENDIX 4.2 COLLINEARITY IN EXPLANATORY COVARIATES

Table A28 Correlation matrix showing correlation coefficients between candidate explanatory covariates of population breeding success. OC = Onshore Component. Highly correlated variables highlighted in bold.

	Year	**Laying date**	**February OC**	**Annual mean aspect**
Year	-			
Laying date	-0.33	-		
February OC	-0.18	0.25	-	
Annual mean aspect	**-0.84**	0.06	0.11	-

APPENDIX 4.3 POISSON ANALYSIS OF BREEDING SUCCESS

Table A29 Full model selection table for Poisson Generalised Linear Mixed Models testing for temporal trends and effects of aspect on nest breeding success and Poisson Generalised Linear Mixed Models testing for temporal trends and drivers of population breeding success. Population breeding success is fitted with a log(number of nests year^{-1}) offset. Table shows model rank compared to other models, model structure, effect sizes (Est), standard errors (SE), number of parameters (k), difference in AICc between top model and selected model (Δ AICc) and Akaike weight relative to other models (ωi). Due to the large numbers of models, effect sizes are only shown for models within 2 AICc points of the top model. Nest aspect presented as south-west (SW) relative to north-east of the island in models of nest-level breeding success. Top models are shown in **bold**. Models with similar levels of support indicated with †. Feb OC = February Onshore Component.

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
Nest breeding success	**1**	***Year + Nest aspect***				**4**	**0.00**	**0.48**
		Year	**0.22**	**0.08**	**2.86**			
		Nest aspect	**-0.11**	**0.02**	**-5.28**			
		Year * Nest aspect	**-0.03**	**0.02**	**-1.41**			
	2	*Year + Nest aspect + Year * Nest aspect*				5	0.04	0.47
	3	*nest aspect*				4	4.53	0.05
	4	*Year*				4	26.55	<0.01
	5	*i*				3	31.30	<0.01
Population breeding success	**1**	***Year + Laying date***				**5**	**0.00**	**0.40**
		Year	**0.17**	**0.07**	**2.32**			
		Laying date	**-0.24**	**0.07**	**-3.29**			
	2	*Year + Feb OC + Laying date*				6	1.70	0.17
	3†	*Laying date*				4	1.79	0.16
		Laying date	-0.30	0.08	-3.87			
	4	*Laying date + Annual mean aspect*				5	2.06	0.14
	5	*Feb OC + Laying date*				5	3.97	0.05
	6	*Feb OC + Laying date + Annual mean aspect*				6	4.13	0.05
	7	*Year*				4	5.88	0.02
	8	*Year + Feb OC*				5	8.66	0.01
	9	*i*				3	10.59	<0.01
	10	*Annual mean aspect*				4	11.14	<0.01

Response	Rank	Model	Est	SE	z	k	ΔAICc	ω_i
	11	*Feb OC*				4	13.29	<0.01
	12	*Feb OC + Annual mean aspect*				5	14.15	<0.01

APPENDIX 4.4 BHATTACHARYYA'S AFFINITY INDICES

Table A30 Pairwise Bhattacharyya's affinity for core areas (50%) of all breeding events between years.

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1994	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1995	0.78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1996	0.76	0.87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1997	0.71	0.87	0.94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1998	0.73	0.85	0.92	0.94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1999	0.67	0.78	0.86	0.89	0.82	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2000	0.73	0.88	0.94	0.92	0.91	0.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2001	0.73	0.82	0.89	0.87	0.86	0.81	0.93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2002	0.71	0.80	0.79	0.81	0.80	0.73	0.8	0.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2003	0.72	0.79	0.80	0.79	0.76	0.76	0.83	0.84	0.78	-	-	-	-	-	-	-	-	-	-	-	-	-
2004	0.64	0.71	0.69	0.68	0.65	0.62	0.74	0.78	0.72	0.87	-	-	-	-	-	-	-	-	-	-	-	-
2005	0.58	0.57	0.56	0.53	0.50	0.56	0.6	0.65	0.63	0.76	0.82	-	-	-	-	-	-	-	-	-	-	-
2006	0.60	0.70	0.64	0.66	0.59	0.69	0.69	0.70	0.62	0.85	0.87	0.88	-	-	-	-	-	-	-	-	-	-
2007	0.58	0.66	0.59	0.61	0.53	0.65	0.64	0.64	0.57	0.81	0.83	0.89	0.97	-	-	-	-	-	-	-	-	-
2008	0.54	0.64	0.58	0.62	0.53	0.64	0.63	0.64	0.56	0.80	0.82	0.83	0.94	0.94	-	-	-	-	-	-	-	-
2009	0.57	0.67	0.61	0.63	0.56	0.66	0.66	0.67	0.60	0.83	0.85	0.83	0.94	0.93	0.91	-	-	-	-	-	-	-
2010	0.57	0.67	0.62	0.64	0.57	0.66	0.66	0.68	0.64	0.80	0.81	0.87	0.93	0.92	0.90	0.90	-	-	-	-	-	-
2011	0.58	0.65	0.63	0.61	0.58	0.63	0.67	0.68	0.65	0.82	0.83	0.84	0.89	0.86	0.86	0.85	0.92	-	-	-	-	-
2012	0.58	0.67	0.61	0.63	0.56	0.66	0.65	0.67	0.64	0.82	0.83	0.81	0.92	0.91	0.90	0.89	0.92	0.91	-	-	-	-
2013	0.59	0.64	0.61	0.59	0.56	0.56	0.64	0.64	0.59	0.77	0.77	0.75	0.78	0.81	0.76	0.75	0.79	0.85	0.85	-	-	-
2014	0.54	0.63	0.57	0.59	0.52	0.61	0.61	0.61	0.58	0.69	0.69	0.67	0.73	0.75	0.70	0.73	0.73	0.74	0.82	0.87	-	-
2015	0.63	0.64	0.63	0.60	0.56	0.58	0.67	0.71	0.60	0.70	0.74	0.77	0.76	0.77	0.72	0.76	0.76	0.75	0.80	0.83	0.88	-

APPENDIX 4.5 EXTENDED MODEL SELECTION TABLE FOR BREEDING SUCCESS

Table A31 Extended model selection table Generalised Linear Mixed Models testing for temporal trends and effects of nest aspect on nest-level breeding success and for Binomial GLMMs testing for temporal trends and drivers of annual breeding success. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z/t values, number of parameters (k), difference in AICc between top model and selected model (Δ AICc) and Akaike weight relative to other models (ωi). Due to the large number of models, we only present those within 2 AICC points of the top model. Nest aspect presented as south-west (SW) relative to north-east of the island. Top models are shown in **bold**. Models with similar levels of support indicated with †. February OC = February Onshore Component.

Response	Rank	Model	k	ΔAICc	ω_i
Nest breeding success	**1**	***Year + Nest aspect + Year*Nest aspect***	**5**	**0.00**	**0.80**
	2	*Year + Nest aspect*	4	2.94	0.18
	3	*Nest aspect*	3	8.29	0.01
	4	*Year*	3	28.24	<0.01
	5	*i*	2	33.79	<0.01
Annual breeding success	**1**	***Year + Laying date***	**4**	**0.00**	**0.40**
	2	*Year + Feb OC + Laying date*	5	1.70	0.17
	3†	*Laying date*	3	1.80	0.16
	4	*Laying date + Annual mean aspect*	4	2.06	0.14
	5	*Feb OC + Laying date*	4	3.97	0.05
	6	*Feb OC + Laying date + Annual mean aspect*	5	4.13	0.05
	7	*Year*	3	5.88	0.02
	8	*Year + Feb OC*	4	8.66	0.01
	9	*i*	2	10.59	<0.01
	10	*Annual mean aspect*	3	11.14	<0.01
	11	*Feb OC*	3	13.29	<0.01
	12	*Feb OC + Annual mean aspect*	4	14.15	<0.01